# The Ecology and Silviculture of *Eucalyptus delegatensis* R.T. Baker on Dolerite in Tasmania.

by

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DECLARATION

This thesis contains no material which has been accepted for the award of any other degree or diploma in any university and contains no copy or paraphases of material previously published or written by another person, except where due reference is made in the text.

D.M.J.S. BOWMAN.

CONTENTS

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ABSTRACT. *Eucalyptus delegatensis* is a widespread dominant of montane forests in southeastern Australia, where is occupies sites of widely varying moisture status and understorey type. The age and size class distributions of *E. delegatensis* on 23 sites of varying precipitation over its range on dolerite in Tasmania are strongly related to the floristic composition of the understorey vegetation and to moisture availability. No stands are even-aged, but all stands exhibit evidence of periodic rather than continuous recruitment; the periodicity of past recruitment events increasing with more mesic conditions. There is evidence for a change towards less frequent recruitment events in the higher rainfall stands since white settlement. An explanation for the variations in regeneration patterns is sought in the complex interactions between climate, fire frequency, fire intensity and understorey vegetation type. The trees in multi-aged forests at the dry end of the environmental range of *E. delegatensis* are extremely fire resistant while the survival of the even-aged saplings is dependent upon their height and bark thickness. Regeneration typically follows forest fire but experimental studies showed that germinates readily establish on cultivated seedbeds. Marked intraspecific competition occurs between the regeneration and the overwood trees. Experiments with germinates, seedlings, and advance growth indicate that soil drought prohibits rapid growth of regeneration beneath overwood while the higher levels of moisture available in forest gaps supports a dense stocking of vigorously growing saplings. Total removal of canopy cover results in a microclimate with greater

maximum and lower minimum ground surface temperatures than in an environmentally similar unlogged stand. The poor health of regeneration on some high altitude clearfelled forest sites is explained by the interactions of canopy cover, frost damage and topography. The various types of eucalypt silvicultural practices are subjectively classified as intensive, partial and selective systems. It is suggested that dry E. delegatensis forests are well suited to selective logging.

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sapling in unburnt forest.

# CHAPTER ONE

## INTRODUCTION

*Eucalyptus delegatensis* R.T. Baker (syn. *Eucalyptus gigantea* Hook. f.) forests form a major component of the Tasmanian sawlog and pulpwood resource. Management of these forests has followed the now normal sequence of clearfelling, slash-burning and aerial sowing of seed (Felton, 1976). However on some high altitude sites the regeneration on cutover and burnt stands has been poor. Such regeneration is described as suffering from growth check, and is characterized by poor apical dominance, small thick leaves, extremely slow growth, and twisted stems and branches. This poor regeneration is a major silvicultural problem given the large area of high altitude forest which is allocated for future forestry operations. A large proportion of this potential timber resource is multi-aged *E. delegatensis* forest on dolerite parent material in central Tasmania. The primary aim of this thesis is to provide ecological data relevant to the sustained exploitation of this forest type.

*Eucalyptus delegatensis* is restricted to south-eastern Australia (Chippendale and Wolf, 1981). On the Australian mainland it typically occupies mountainous areas between 1000-1400 m A.S.L. that receive about 1000-1500 mm of precipitation annually. In Tasmania it occurs between 300-1300 m A.S.L. with increasing upper and lower altitudinal limits in more continental localities. The species occupies a variety of topographic positions, is tolerant of a range of precipitation

(700-2900 mm) and grows on soils ranging from infertile brown fibrous peats over quartzite to fertile krasnozems on basalt. Stands of the species have a large variety of understorey synusiae, including temperate rainforest, broad-leaf scrub, heath, fernland, grassland and sedgeland.

The ecology of the tall open E. delegatensis forests is believed to be similar to that of E. regnans forests (Cremes, et. al., 1978). Both monocalypt species are non-lignotuberous, and are thought to form even-aged stands following infrequent intense wildfire which destroys the dense understorey and kills the overwood (Grose, 1957; Gilbert, 1959). Autecological studies of E. delegatensis wet sclerophyll forests have focused on the factors affecting seedling establishment following logging (Grose,1957, 1960a, 1960b, 1961, 1963; Orme, 1971), the nature of the premature mortality of stands with young temperate rainforest understoreys (Ellis, 1964, 1971; Ellis et al., 1980), and the slow growth of regeneration on intensively logged high altitude sites (Webb et al. ,1983;Keenan and Candy,1984).

Multi-aged E. delegatensis forests and woodlands have been reported on the Australian mainland (Costin, 1954; Costin et al., 1959; Chesterfield,1978). These stands are considered to be a climax condition produced by the senescence of the broad-leaf understorey and maintained by gap phase replacement (Costin, 1954; Park, 1976; Harwood, 1976; Shugart and Noble, 1981) or by cool fires (Chesterfield, 1978). Similar multi-aged E. delegatensis in high rainfall areas of Tasmania have been

described as a fire sere in the succession from grassland to temperate rainforest (Ellis, 1964; Orme, 1971).

Multi-aged E. delegatensis open forests with heath understoreys are restricted to Tasmania. This limitation may be due to genetic variation between mainland and Tasmanian populations. For example, the mainland form has lanceolate adult leaves, fibrous bark covering the lower half of the trunk, poor vegetative recovery following damage and is extremely fire sensitive. In contrast, the Tasmanian form has ovate adult leaves, readily coppices from stumps, fibrous bark covering at least the lower third of the stem and often up to the the base of the branches in the crown, is extremely fire resistant, and can persist as a suppressed lignotuberous-like seedling in the dry sclerophyll understorey for up to 30 years. Perhaps the non-lignotuberous eucalypt most analogous to Tasmanian E. delegatensis is Eucalyptus pilularis. This species has a similar wide ecological range and also forms suppressed advance growth in the understorey of dry forests (Cremer et al., 1978).

Although multi-aged open eucalypt forests have a long history of exploitation, and currently support woodchip industries in three states, surprisingly little is known of their natural regeneration processes. General models have been proposed (e.g. Mount, 1979) but no detailed studies have been published. The following three chapters report demographic studies of multi-aged E. delegatensis forests on dolerite in Tasmania. Chapter five considers the microclimatic impact of

canopy removal on forest regeneration. The concluding chapter discusses natural regeneration processes in this forest type and, in the light of the available information, considers various silvicultural options.

# CHAPTER TWO

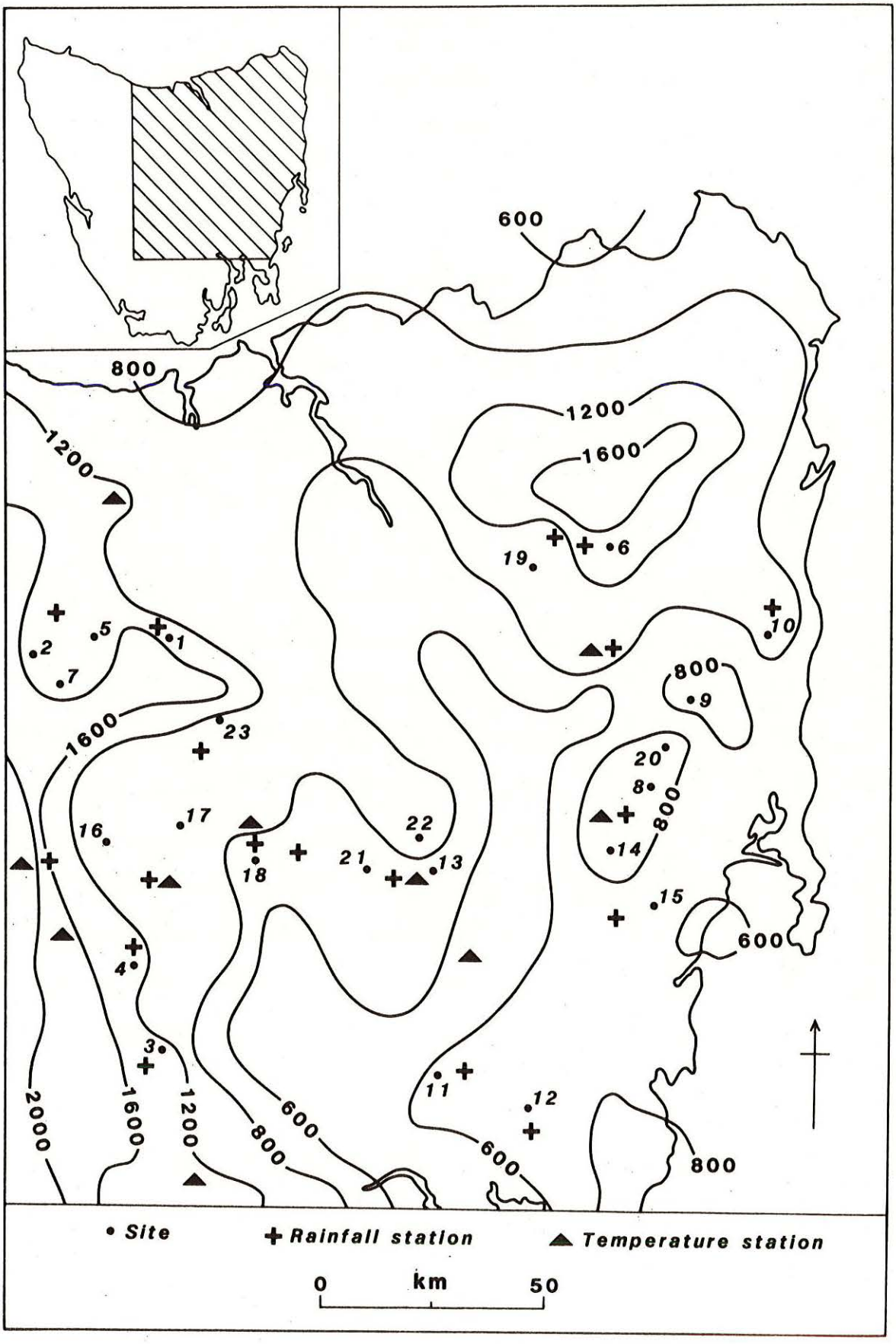
## GEOGRAPHIC VARIATION OF E. DELEGATENSIS STAND DEMOGRAPHY

### 2.1 INTRODUCTION

The longevity of tree species precludes direct observation of their stand demography. However, analysis of age structure for a given time slice can reveal the mode of regeneration of a stand. For example, Gilbert (1959) demonstrated that E. regnans only regenerates after wildfire which destroys the mature forest. This dependence of regeneration on fire has been generalized to most other tall open eucalypt forests with dense understoreys (Cremer et al., 1978). The demography of multi-aged eucalypt forests with open understoreys has received little attention (Gill and Ashton, 1971; Duncan, 1981). Similarly, the intraspecific variation of regeneration processes of eucalypt species with a wide ecological range has not been reported in the literature. The aim of this chapter is to determine the relationship between stand environment, understorey type( ranging from temperate rainforest to open heath) and the mode of regeneration of E. delegatensis forests on Jurassic dolerite.

### 2.2 DATA COLLECTION

Data were collected from 23 sites throughout the climatic range of E. delegatensis on dolerite parent material in Tasmania (Figure 2.1). Each site encompassed part of a clearfelled coupe plus adjacent unmodified forest in a closely similar topographic and edaphic environment. At each site the diameter at about 50 cm above the ground and ring number were measured for fifty


600
800
1200
1600
1200
1600
800
800
600
600
800
2000
1600
1200
600
800
600
800
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
• Site
+ Rainfall station
▲ Temperature station
0
km
50

randomly selected stumps greater than 10 cm diameter, except where the inner part of the stump was rotted, in which case only diameter was measured. The diameter and species of all living and dead eucalypts with diameters greater than 10 cm were noted for a 30 x 15 m plot in the unmodified forest. Up to 36 *E. delegatensis* individuals of less than 10 cm diameter were collected from a contiguous area within the unlogged stand, the age and diameter of each stem being determined after sectioning at the stem base and examination of the rings under a binocular microscope.

The height of the unmodified forest was measured using clinometer and tape. Three hemispherical photographs were used to estimate projective foliage cover using the method of Steyn (1980). The cover, density and mean height of all woody species were measured within ten 5 x 5 m quadrats for those more than 5 m tall and ten 2 x 2 m quadrats for those less than 5 m tall. The percentage cover of bracken (*Pteridium esculentum*), other ferns, grass, other graminoids, forbs, moss, litter, rocks and bare ground were estimated for ten 1 x 1 m quadrats. All of the above quadrats were located by random numbers within the 30 x 15 m plot.

Slope and slope aspect were measured with a clinometer and a compass. Altitude was obtained from the 1:100,000 map series to the nearest 20 m. The topographic positions were classified as one of: gully, scarp base, scarp slope, scarp top, plateau, knoll. Precipitation variables were obtained by interpolation of

data from statistics and maps available from the Australian Bureau of Meteorology. Temperature values were calculated from data from the most appropriate nearby station (Figure 2.1) by applying the empirically derived environmental lapse rates: January mean daily maximum temperature = -0.87°C per 100m, July mean daily minimum temperature = -0.42°C per 100m (Nunez, pers. comm.,1981)

At each site the colours of the duff layer, mineral top soil (0-15 cm) and mineral subsoil (60-80 cm) were recorded using a standard soil colour chart. Duff depth was measured and bulked samples were obtained for the mineral topsoil and subsoil. Soil texture (sand 2.0-0.02 mm, silt 0.02-0.002 and clay < 0.002) was determined using the hydrometer method described by Day (1965). The < 2 mm top soil sample was analysed for: organic matter by loss on ignition at 600°C; total nitrogen following Kjeldahl digestion; total phosphorus by the Vanodo-molybdate method; potassium, sodium and calcium by flame emission measurement on an EEl flame photometer; magnesium by flame atomic absorption on a Varian 1200; and pH using a T.P.S. meter with a 20% de-ionised water suspension.

A petrological thin section was prepared from a specimen of unweathered dolerite and the felsic index (McDougall, 1962, figure 2.5) was calculated after the estimation of the proportion of pyroxene by slide traverse.

## 2.3 DATA ANALYSIS

Linear regressions were calculated for each site with the dependent variable age against the independent variable diameter. If a poor relationship was obtained $\log_e$ transformed data was regressed to find whether the strength of the relationship could be improved (Veblen et al., 1980). For each site the age of measured stems with rotted centres was estimated using the most significant regression equation. Age and size class histograms were drawn for the trees (>10cm dbhob) and saplings (<10 cm dbhob) at each site with the respective class intervals being 10 year or cm and 2 year or cm. A single value characterizing the age structure of each stand (stand demographic index) was obtained by finding the correlation coefficient between the number of stems and the corresponding 10 year age class following the linear transformation of the power function

$$y = y_o x^{-b}$$

where y is the number in any age class x, $y_o$ is the initial number of stems at time zero and b is the mortality rate (Hett and Loucks, 1976). Through the application of the above method Veblen et al., (1979 and 1980) interpreted a significant correlation with the reverse J curve as evidence of continuous regeneration, while a poor correlation was seen as evidence of phasic recruitment.

A single axis polar ordination was performed, using a scale

of 1-6 (=+-5 in the Braun-Blanquet cover abundance scale) for individual woody species cover and ground cover. Stands 2 and 18 were used as poles following the method of Bray and Curtis (1957).This gave a single value for the understorey vegetation at each site. Using the same similarity measure employed in the above ordination, an average linkage cluster analysis of the 23 stands was also performed.

All possible interrelations between the stand demographic structure index, the ordination score and the environmental variables listed in Table 2.1 were analysed by generating a correlation matrix. A stepwise multiple linear regression was performed with stand structure as the dependent variable and characters 2-11 (Table 2.1) as the independent variables. The most significant predictor from this analysis was used as the dependent variable in a subsequent stepwise multiple regression analysis in which the independent variables were characters 3-14 (Table 2.1).

## 2.4 RESULTS

Age and diameter are significantly correlated within all stands for both trees and saplings. This relationship is stronger for trees than for saplings for most sites (Tables 2.2 and 2.3).

The age class distributions for all stands are irregular and multimodal (Figure 2.2 and Table 2.4). The frequent phases of recruitment are usually well-separated from other periods of recruitment. This is clearly shown for saplings in Table 2.4.

TABLE 2.1

Environmental variables determined for each site. The codes are used in Figure 2.6

| Number | Variable | Codes |
|---|---|---|
| 1 | Stand structure r | STDR |
| 2 | Ordination | ORD |
| 3 | Sky view factor | SVF |
| 4 | Altitude | ALT |
| 5 | Maximum temperature | MAXT |
| 6 | Minimum temperature | MINT |
| 7 | Difference between max.and min. temp | DIFT |
| 8 | Annual rainfall | YR |
| 9 | Rainfall in driest month | DMR |
| 10 | Annual rainfall evenness ratio[1] | DW |
| 11 | pH | pH |
| 12 | Topographic position | TOP |
| 13 | Aspect | ASP |
| 14 | Slope | S |
| 15 | Depth of organic matter | DUFF |
| 16 | Felsic index | FI |
| 17 | Height of stand | H |
| 18 | Basal area | BA |
| 19 | Density of stem > 10 cm diameter | D>10 |
| 20 | Density of stems < 10 cm diameter | D<10 |
| 21 | % Clay in topsoil | CT |
| 22 | % Silt in topsoil | SIT |
| 23 | % Sand in topsoil | SAT |
| 24 | % Clay in subsoil | CS |
| 25 | % Silt in subsoil | SIS |
| 26 | % Sand in subsoil | SS |
| 27 | Organic matter in topsoil | OM |
| 28 | Total phosphorus in topsoil | P |
| 29 | Total nitrogen in topsoil | N |
| 30 | Total sodium in topsoil | Na |
| 31 | Total potassium in topsoil | K |
| 32 | Total calcium in topsoil | Ca |
| 33 | Total magnesium in topsoil | Mg |

1. Rainfall in driest month/rainfall in wettest month.

Plate 2.1. Foliage cover, understorey vegetation and stand profile at site 1.

TABLE 2.2

Regressions used to predict age (y) of tree stumps with rotted centres at each site.

| Site No. | Regression equation | r | Sig. | n |
|---|---|---|---|---|
| 1 | $y = 58.3 + 0.9x$ | 0.55 | P<0.001 | 45 |
| 2 | $\log_e y = 2.2+0.6 \log_e x$ | 0.80 | P<0.001 | 36 |
| 3 | $\log_e y = 0.5+1.0 \log_e x$ | 0.92 | P<0.001 | 32 |
| 4 | $y = -5.3 + 1.5x$ | 0.95 | P<0.001 | 50 |
| 5 | $y = 14.5 + 0.9x$ | 0.91 | P<0.001 | 30 |
| 6 | $y = 22.4 + 1.6x$ | 0.95 | P<0.001 | 48 |
| 7 | $y = 13.6 + 0.9x$ | 0.90 | P<0.001 | 46 |
| 8 | $y = 24.0 + 1.5x$ | 0.85 | P<0.001 | 35 |
| 9 | $y = 12.3 + 1.4x$ | 0.90 | P<0.001 | 47 |
| 10 | $y = 21.7 + 1.9x$ | 0.93 | P<0.001 | 48 |
| 11 | $y = 4.6 + 0.7x$ | 0.95 | P<0.001 | 40 |
| 12 | $Y = 24.6 + 1.4x$ | 0.74 | P<0.001 | 43 |
| 13 | $y = 14.6 + 1.5x$ | 0.81 | P<0.001 | 48 |
| 14 | $y = 32.1 + 1.1x$ | 0.80 | P<0.001 | 44 |
| 15 | $y = 36.3 + 1.1x$ | 0.77 | P<0.001 | 40 |
| 16 | $y = 17.5 + 1.8x$ | 0.93 | P<0.001 | 48 |
| 17 | $y = 34.7 + 1.2x$ | 0.82 | P<0.001 | 49 |
| 18 | $y = 41.5 + 0.5x$ | 0.77 | P<0.001 | 36 |
| 19 | $y = 28.2 + 1.0x$ | 0.82 | P<0.001 | 49 |
| 20 | $y = 6.2 + 2.1x$ | 0.80 | P<0.001 | 44 |
| 21 | $y = 35.3 + 1.3x$ | 0.74 | P<0.001 | 49 |
| 22 | $y = 20.6 + 1.8x$ | 0.86 | P<0.001 | 49 |
| 23 | $y = 22.6 + 0.8x$ | 0.76 | P<0.001 | 46 |

TABLE 2.3

Relationship between the age (y) and stem base diameter (x) of saplings (<10cm d.b.h.o.b.) at each site.

| Site No. | Regression equation | r | Sig. | n |
|---|---|---|---|---|
| 1 | | | | |
| 2 | | | | |
| 3 | | | | |
| 4 | $y = 15.2 + 0.6x$ | 0.68 | $P<0.01$ | 14 |
| 5 | | | | |
| 6 | | | | |
| 7 | $y = 24.2 + 1.2x$ | 0.69 | $P<0.01$ | 13 |
| 8 | $y = 5.6 + 3.2x$ | 0.88 | $P<0.001$ | 22 |
| 9 | | | | |
| 10 | $y = 8.3 + 1.6x$ | 0.66 | $P<0.01$ | 23 |
| 11 | $y = 9.0 + 1.6x$ | 0.69 | $P<0.001$ | 34 |
| 12 | $y = 5.4 + 2.1x$ | 0.72 | $P<0.001$ | 31 |
| 13 | $y = 3.9 + 3.7x$ | 0.96 | $P<0.001$ | 14 |
| 14 | $y = 6.3 + 1.7x$ | 0.74 | $P<0.001$ | 19 |
| 15 | $y = 7.0 + 2.0x$ | 0.83 | $P<0.001$ | 27 |
| 16 | $y = 4.5 + 4.1x$ | 0.82 | $P<0.001$ | 18 |
| 17 | $y = 6.1 + 3.9x$ | 0.74 | $P<0.05$ | 9 |
| 18 | $y = 6.4 + 3.5x$ | 0.79 | $P<0.001$ | 36 |
| 19 | $y = 4.1 + 4.2x$ | 0.93 | $P<0.001$ | 9 |
| 20 | $y = 4.7 + 2.5x$ | 0.97 | $P<0.001$ | 8 |
| 21 | $y = 4.6 + 3.8x$ | 0.85 | $P<0.001$ | 28 |
| 22 | $y = 5.3 + 4.1x$ | 0.62 | $P<0.001$ | 30 |
| 23 | $y = 7.7 + 2.3x$ | 0.83 | $P<0.001$ | 19 |

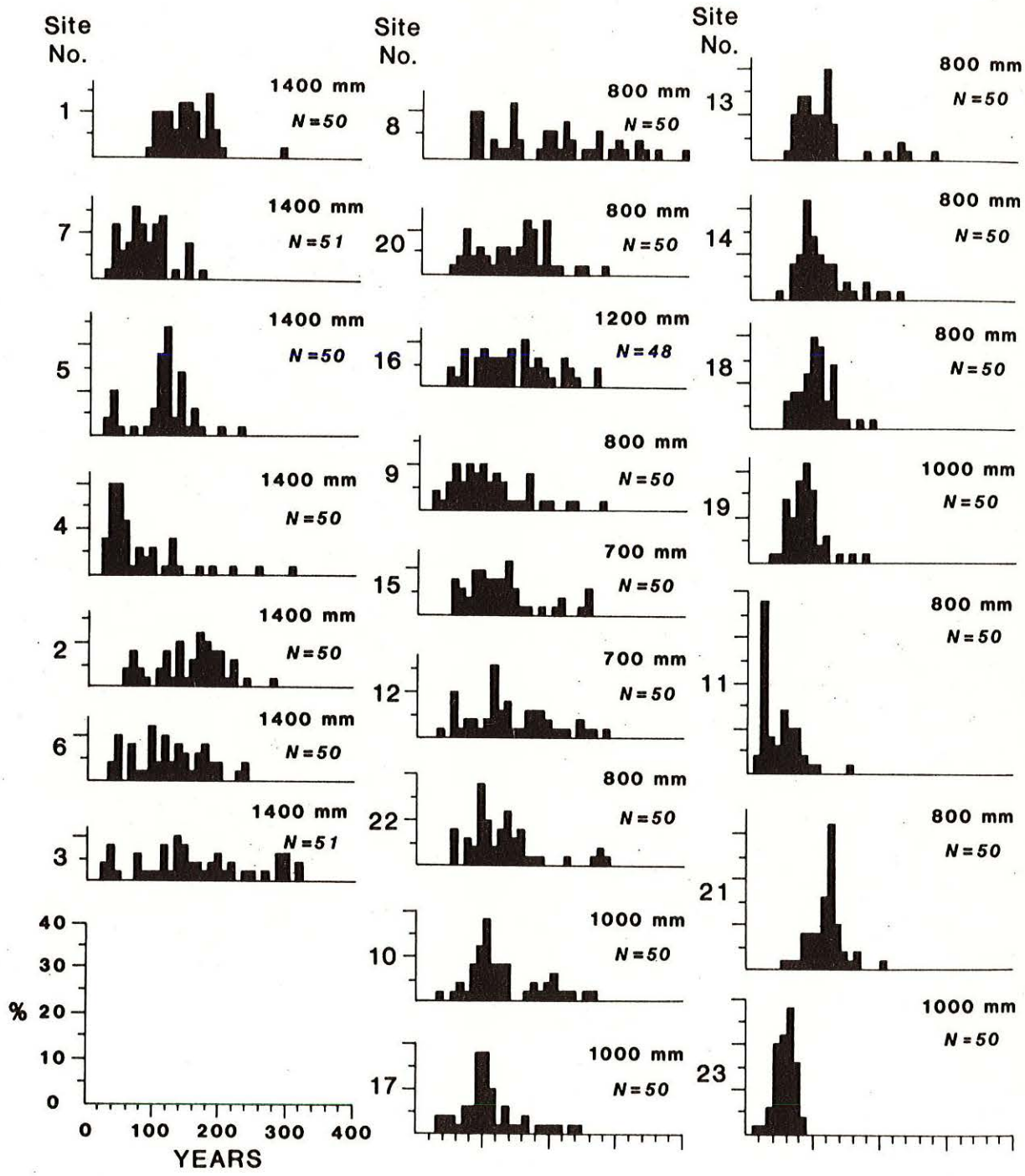
TABLE 2.4

Percentage frequency and number of saplings (<10 cm d.b.h.o.b.) grouped in six year age classes, by site.

| Site No. | 1-6 | 6-12 | 12-18 | 18-24 | 24-30 | 30-36 | 36-42 | N |
|---|---|---|---|---|---|---|---|---|
| 1 | - | - | - | - | - | - | - | 0 |
| 2 | - | - | - | - | - | - | - | 0 |
| 3 | - | - | - | - | - | - | - | 0 |
| 4 | - | - | 33 | 65 | - | - | - | 14 |
| 5 | - | - | - | - | - | - | - | 0 |
| 6 | - | - | - | - | - | - | - | 0 |
| 7 | - | - | - | - | 62 | 31 | 8 | 13 |
| 8 | - | 81 | 19 | - | - | - | - | 22 |
| 9 | - | 100 | - | - | - | - | - | 2 |
| 10 | 4 | 75 | 17 | 4 | - | - | - | 24 |
| 11 | | 56 | 41 | 3 | - | - | - | 34 |
| 12 | 13 | 81 | 6 | - | - | - | - | 31 |
| 13 | 43 | 35 | 7 | 14 | - | - | - | 14 |
| 14 | 5 | 90 | 5 | - | - | - | - | 20 |
| 15 | - | 74 | 26 | - | - | - | - | 27 |
| 16 | 17 | 45 | 22 | 17 | - | - | - | 18 |
| 17 | - | - | 55 | 33 | 11 | - | - | 9 |
| 18 | - | 81 | 19 | - | - | - | - | 36 |
| 19 | 11 | 78 | 11 | - | - | - | - | 9 |
| 20 | 38 | 50 | 12 | - | - | - | - | 8 |
| 21 | 54 | 43 | 3 | - | - | - | - | 28 |
| 22 | 60 | 36 | 4 | - | - | - | - | 30 |
| 23 | - | 58 | 42 | - | - | - | - | 19 |

Figure 2.1. The location of study sites ,average annual rainfall isohyets (mm),and associated meterological stations.

Figure 2.2. Percentage frequency histograms of trees (>10 cm diameter) grouped in 10 year classes and mean annual precipitation.


Site No.
Site No.
Site No.
1
1400 mm
N=50
7
1400 mm
N=51
5
1400 mm
N=50
4
1400 mm
N=50
2
1400 mm
N=50
6
1400 mm
N=50
3
1400 mm
N=51
8
800 mm
N=50
20
800 mm
N=50
16
1200 mm
N=48
9
800 mm
N=50
15
700 mm
N=50
12
700 mm
N=50
22
800 mm
N=50
10
1000 mm
N=50
17
1000 mm
N=50
13
800 mm
N=50
14
800 mm
N=50
18
800 mm
N=50
19
1000 mm
N=50
11
800 mm
N=50
21
800 mm
N=50
23
1000 mm
N=50
40
30
% 20
10
0
0
100
200
300
400
YEARS

Several sources of error however, lead to difficulty in precisely identifying discrete regeneration events from Figure 2.2. These sources include : variation in stump height and, the growth rate of the trees (Figure 2.10); observer error, false or fused growth rings, and interpolation from the age-diameter regressions.

In Figure 2.2 the stands are subjectively divided into three groups : those occurring in areas where annual precipitation exceeds 1300 mm (Plate 2.1); those with a distinct recruitment peak and from drier areas (Plates 2.2 and 2.3); and those with no distinct recruitment peak and from drier areas(Plate 2.4). Most of the more mesic stands lack the sapling class, in marked contrast to the stands in the drier areas (Table 2.4). However, there is no discernible difference between the age class structures of stands in wet and dry areas for the part of each histogram which indicates establishment prior to the decline of the aboriginal population 160 years ago.

The stand demography structure index divided the stands into two clear groups; one in which the value of r was less than 0.3 and in which the sapling class was absent or sparse (i.e. site 19), and one in which the value of r was greater than 0.6 and the sapling class was present (Table 2.4,2.5).

The weak clustering of the agglomerative classification is consistant with the idea that the stands were sampled from a continuum of understorey and ground covers (Figure 2.3). The

Figure 2.3. Dendrogram showing the agglomerative classification of sites.

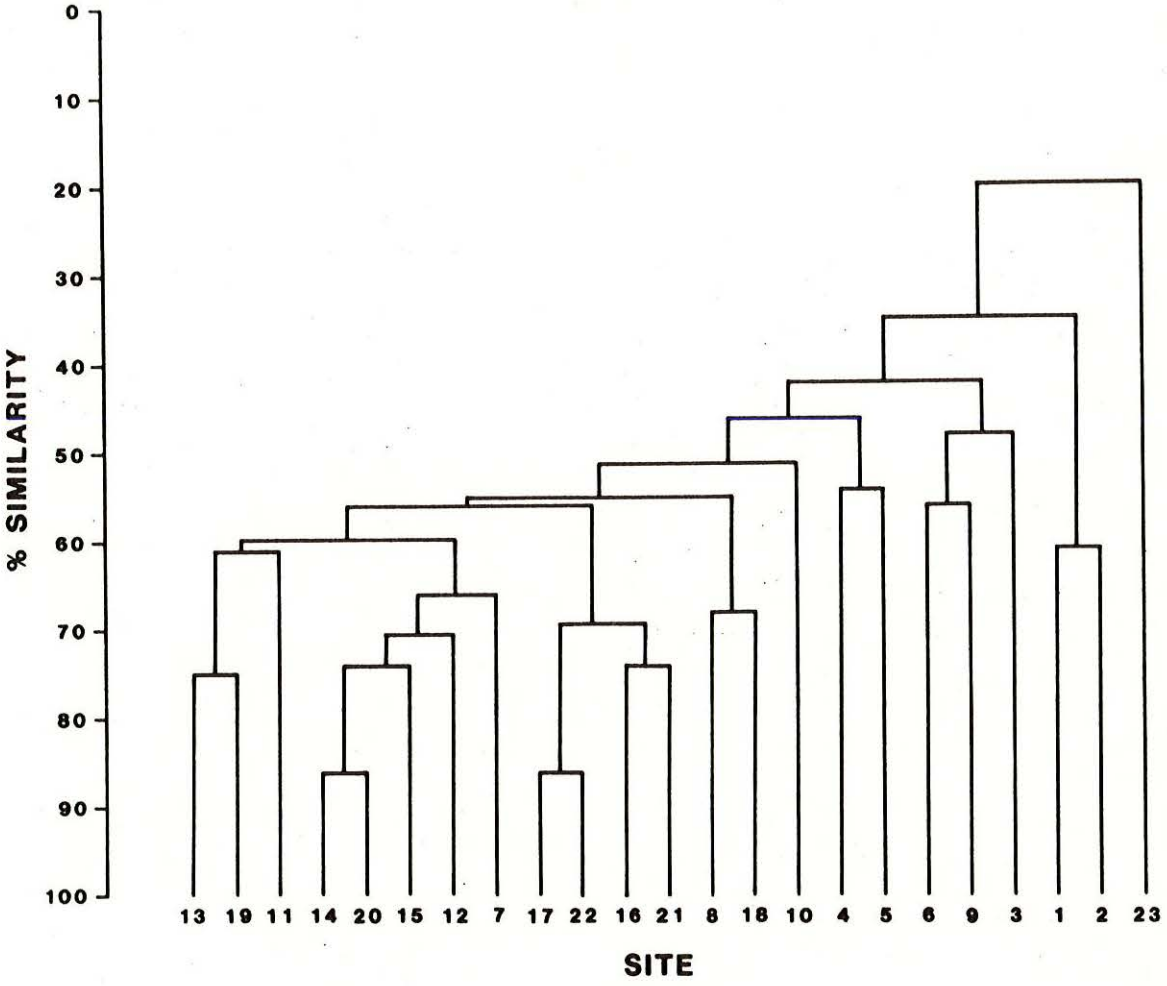

% SIMILARITY
0
10
20
30
40
50
60
70
80
90
100
13 19 11 14 20 15 12 7 17 22 16 21 8 18 10 4 5 6 9 3 1 2 23
SITE

Figure 2.4. Cover of woody understorey species across the ordination gradient.

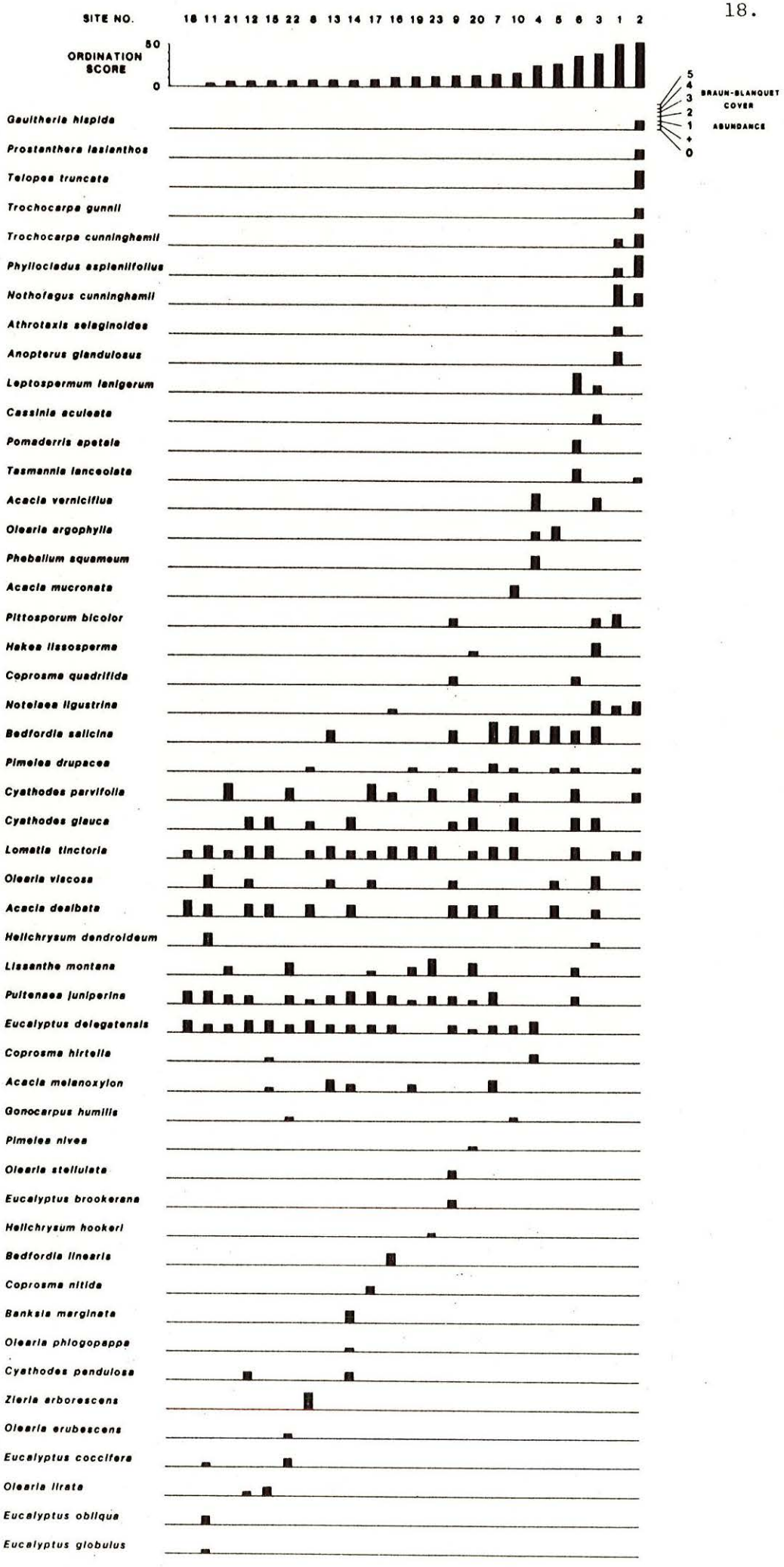

SITE NO.
18 11 21 12 15 22 8 13 14 17 16 19 23 9 20 7 10 4 5 6 3 1 2
ORDINATION SCORE
50
0
5
4
3
2
1
+
0
BRAUN-BLANQUET COVER ABUNDANCE
Gaultheria hispida
Prostanthera lasianthos
Telopea truncata
Trochocarpa gunnii
Trochocarpa cunninghamii
Phyllocladus asplenifolius
Nothofagus cunninghamii
Athrotaxis selaginoides
Anopterus glandulosus
Leptospermum lanigerum
Cassinia aculeata
Pomaderris apetala
Tasmannia lanceolata
Acacia verniciflua
Olearia argophylla
Phebalium squameum
Acacia mucronata
Pittosporum bicolor
Hakea lissosperma
Coprosma quadrifida
Notelaea ligustrina
Bedfordia salicina
Pimelea drupacea
Cyathodes parvifolia
Cyathodes glauca
Lomatia tinctoria
Olearia viscosa
Acacia dealbata
Helichrysum dendroideum
Lissanthe montana
Pultenaea juniperina
Eucalyptus delegatensis
Coprosma hirtella
Acacia melanoxylon
Gonocarpus humilis
Pimelea nivea
Olearia stellulata
Eucalyptus brookerana
Helichrysum hookeri
Bedfordia linearis
Coprosma nitida
Banksia marginata
Olearia phlogopappa
Cyathodes pendulosa
Zieria arborescens
Olearia erubescens
Eucalyptus coccifera
Olearia lirata
Eucalyptus obliqua
Eucalyptus globulus

Figure 2.5. Ground cover across the ordination gradient.

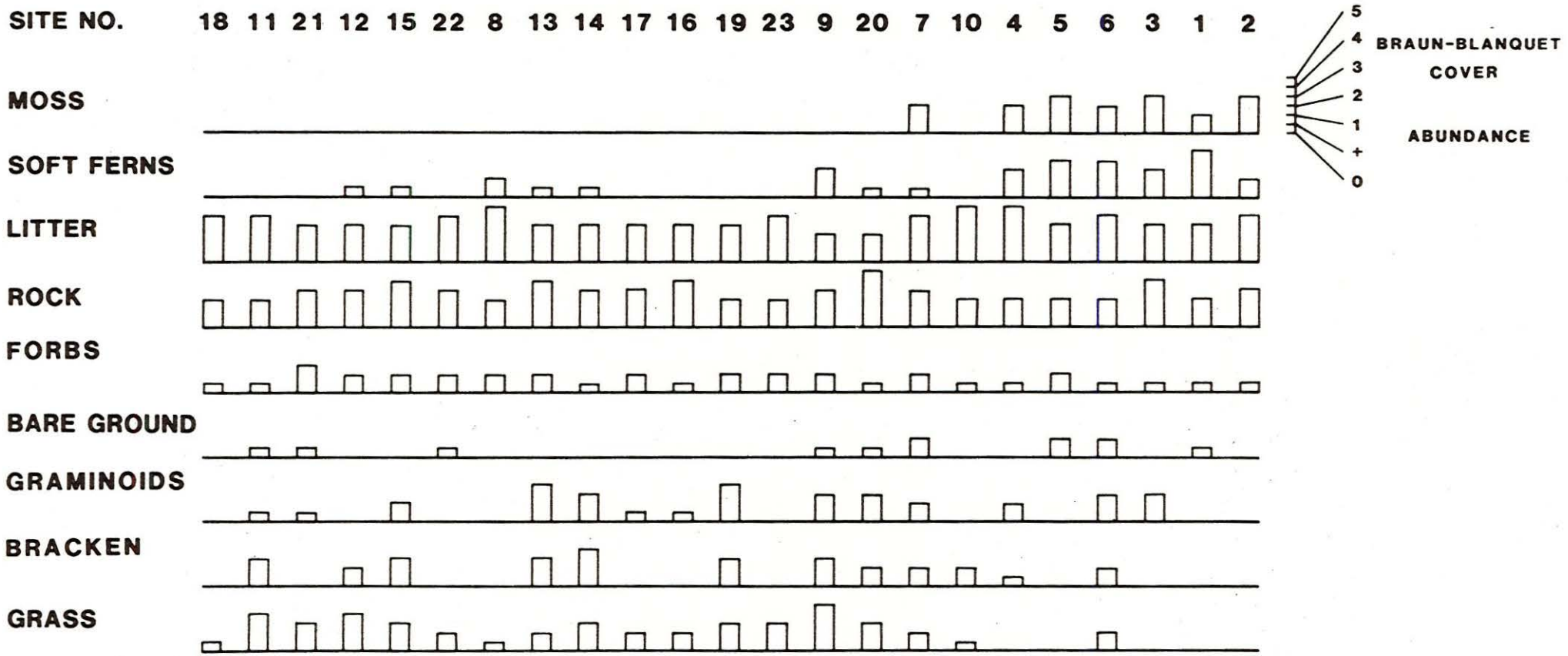

SITE NO.
18 11 21 12 15 22 8 13 14 17 16 19 23 9 20 7 10 4 5 6 3 1 2
MOSS
SOFT FERNS
LITTER
ROCK
FORBS
BARE GROUND
GRAMINOIDS
BRACKEN
GRASS
5
4
3
2
1
+
0
BRAUN-BLANQUET
COVER
ABUNDANCE

TABLE 2.5

Power function regression equations of combined tree and sapling number (y) in 10 year age classes (x) for each site. The presence of saplings is also indicated.

| Site No. | Regression equation | r | sig | n | Saplings Present |
|---|---|---|---|---|---|
| 1 | $y = 90x^{-0.66}$ | 0.30 | NS | 13 | |
| 2 | $y = 3.6x^{-0.09}$ | 0.06 | NS | 18 | |
| 3 | $y = 2.4x^{-0.06}$ | 0.07 | NS | 24 | |
| 4 | $y = 339.3x^{-1.10}$ | 0.85 | P<0.001 | 17 | X |
| 5 | $y = 4.0x^{-0.13}$ | 0.09 | NS | 15 | |
| 6 | $y = 6.5x^{-0.21}$ | 0.19 | NS | 18 | |
| 7 | $y = 26,335x^{-1.94}$ | 0.80 | P<0.001 | 12 | X |
| 8 | $y = 2,650x^{-1.39}$ | 0.89 | P<0.001 | 24 | X |
| 9 | $y = 175.4x^{-0.94}$ | 0.76 | P<0.001 | 21 | X |
| 10 | $y = 127.9x^{-0.85}$ | 0.71 | P<0.001 | 23 | X |
| 11 | $y = 3672x^{-1.66}$ | 0.86 | P<0.001 | 12 | X |
| 12 | $y = 1574x^{-1.36}$ | 0.81 | P<0.001 | 25 | X |
| 13 | $y = 1203x^{-1.25}$ | 0.89 | P<0.001 | 16 | X |
| 14 | $y = 1808x^{-1.38}$ | 0.87 | P<0.001 | 17 | X |
| 15 | $y = 4869x^{-1.55}$ | 0.91 | P<0.001 | 19 | X |
| 16 | $y = 179x^{-0.87}$ | 0.81 | P<0.001 | 21 | X |
| 17 | $y = 450x^{-1.13}$ | 0.73 | P<0.001 | 22 | X |
| 18 | $y = 91,301x^{-2.20}$ | 0.93 | P<0.001 | 14 | X |
| 19 | $y = 4.4x^{-0.12}$ | 0.12 | NS | 14 | X |
| 20 | $y = 203x^{-0.94}$ | 0.77 | P<0.001 | 22 | X |
| 21 | $y = 1,145x^{-1.29}$ | 0.76 | P<0.001 | 15 | X |
| 22 | $y = 1,206x^{-1.26}$ | 0.91 | P<0.001 | 19 | X |
| 23 | $y = 0.3x^{0.72}$ | 0.64 | NS | 9 | X |

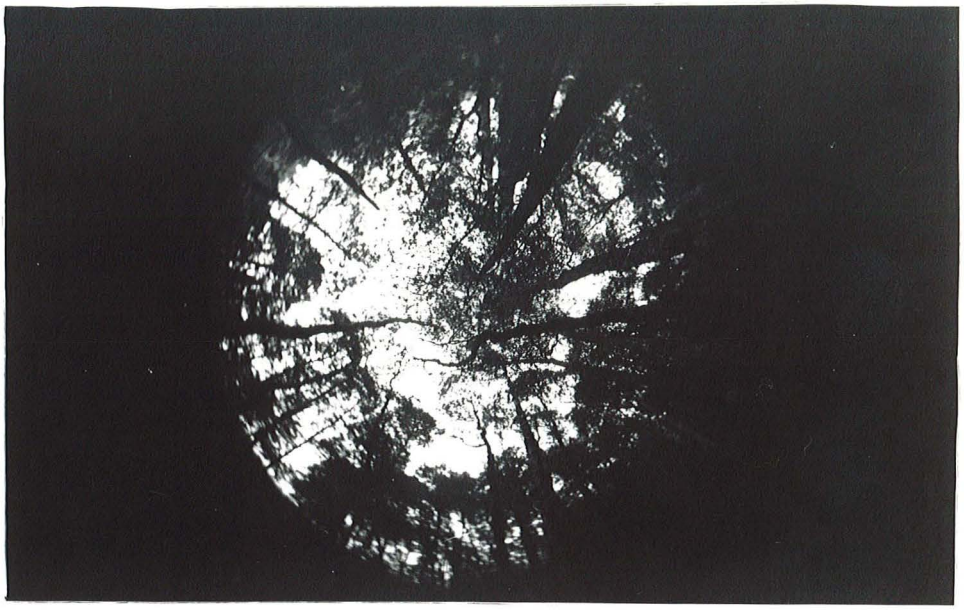


Plate 2.2. Foliage cover, understorey vegetation and stand profile at site 21.

Plate 2.3. Foliage cover, stand profile and understorey vegetation at site 15.

Plate 2.4. Stand profile, foliage cover and understorey vegetation at the Waddamana Research site (site 18).

floristic gradient was clearly described by the polar ordination (Figures 2.4 and 2.5). The ordination score was best accounted for by mean annual precipitation ($r^2$ =0.66) with no other variable achieving significance (P>0.05) in the stepwise regression (Figure 2.6).

The stand ordination score best explains the demographic structure index, accounting for almost two thirds ($r^2$ =0.62) of its variance with no other variable contributing significantly to the explanation level. The constellation diagram (Figure 2.7) indicates the strong mutual relationships between understorey vegetation species composition, precipitation variables and demographic structure. The sky view factor, stand height and most soil variables are either relatively independent of the demographic structure index or more strongly related to the precipitation variables or to the ordination score (Figures 2.6 and 2.7).

The strongly interrrelated understorey vegetation and demographic structure variables are influenced by the interaction between precipitation and fire. The time elapsed since the last fire, as measured from the age of the youngest cohort of regeneration, increases across the rainfall gradient (Figure 2.8). In the seven high annual rainfall stands (c. 1400 mm) the scatter of ordination values is explicable in terms of the last regeneration event (Figure 2.9). Rainfall also affects vegetation type through its impact on the production of biomass which has a feedback effect on fire frequency and the intensity

Figure 2.6. Variation of stand characteristics and environmental variables across the ordination gradient.

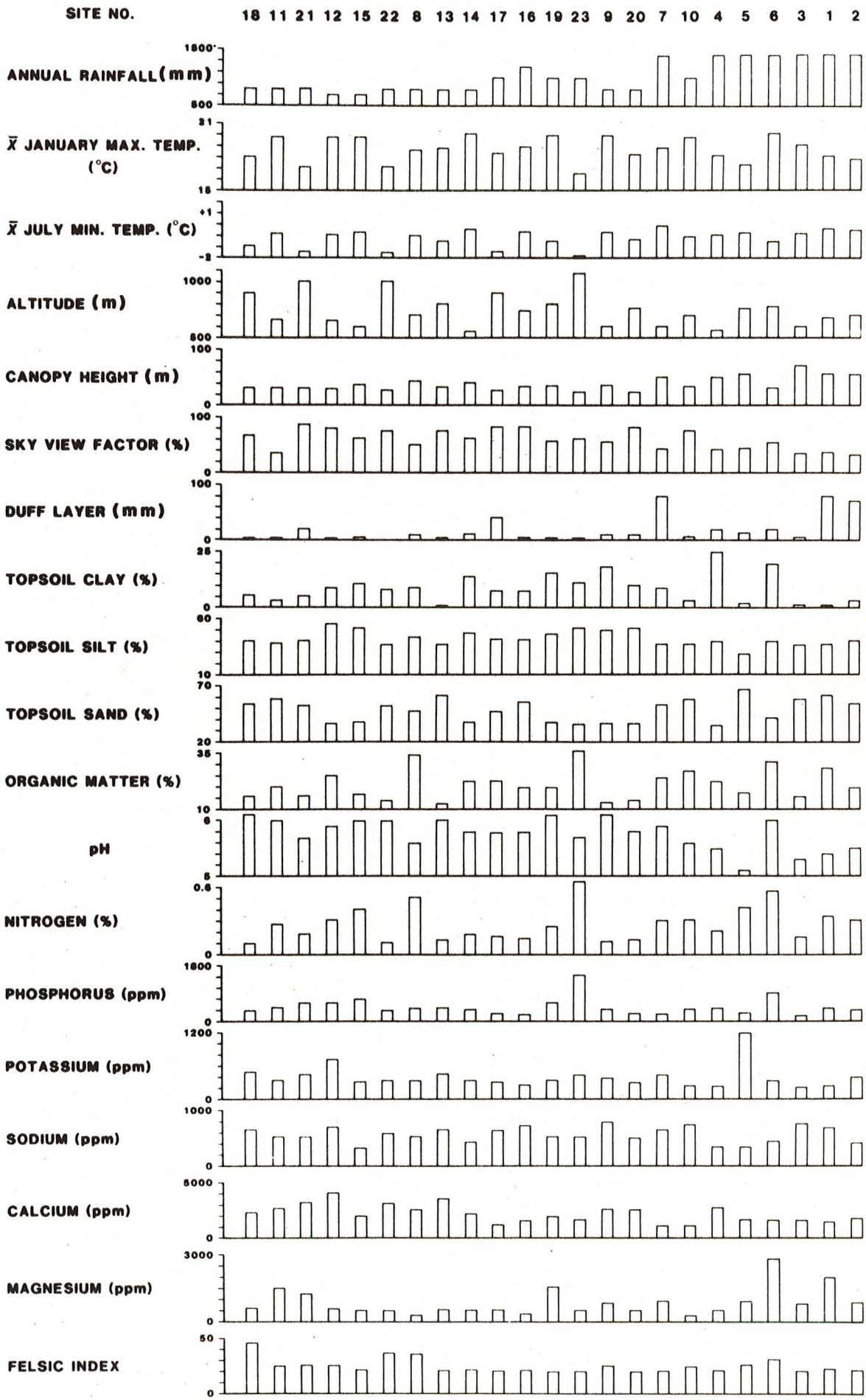

SITE NO.
18 11 21 12 15 22 8 13 14 17 16 19 23 9 20 7 10 4 5 6 3 1 2
ANNUAL RAINFALL (mm)
1600
800
X̄ JANUARY MAX. TEMP. (°C)
21
15
X̄ JULY MIN. TEMP. (°C)
+1
-2
ALTITUDE (m)
1000
800
CANOPY HEIGHT (m)
100
0
SKY VIEW FACTOR (%)
100
0
DUFF LAYER (mm)
100
0
TOPSOIL CLAY (%)
25
0
TOPSOIL SILT (%)
60
10
TOPSOIL SAND (%)
70
20
ORGANIC MATTER (%)
35
10
pH
6
5
NITROGEN (%)
0.6
0
PHOSPHORUS (ppm)
1600
0
POTASSIUM (ppm)
1200
0
SODIUM (ppm)
1000
0
CALCIUM (ppm)
5000
0
MAGNESIUM (ppm)
3000
0
FELSIC INDEX
50
0

Figure 2.7. Constellation diagram showing significant relationships ($p < 0.01$) of environmental variables by site. Key to variable abbreviations in Table 2.1.

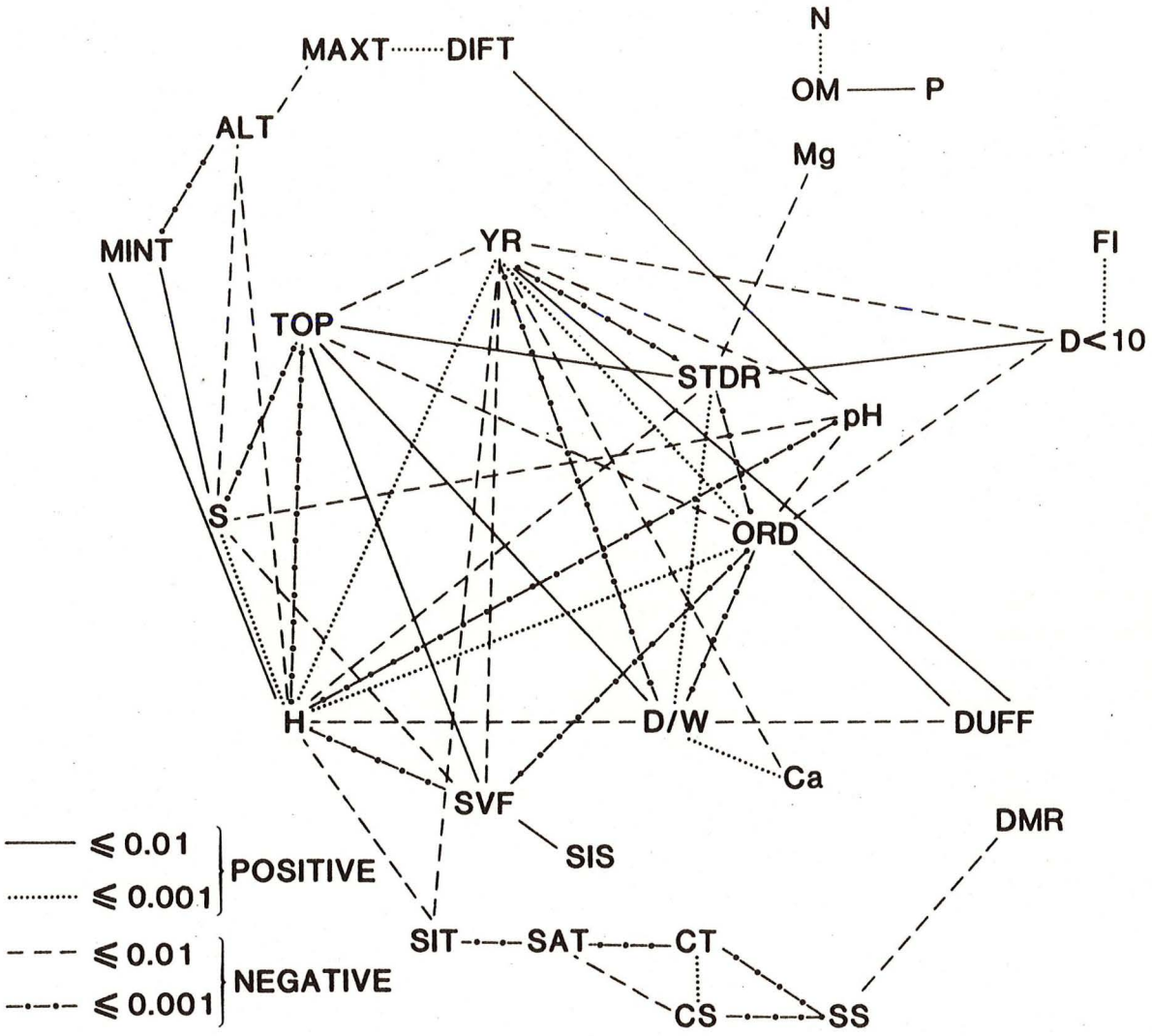

N
MAXT
DIFT
OM
P
ALT
Mg
MINT
YR
FI
TOP
D<10
STDR
pH
S
ORD
H
D/W
DUFF
Ca
SVF
SIS
DMR
SIT
SAT
CT
CS
SS
≤ 0.01
≤ 0.001
POSITIVE
≤ 0.01
≤ 0.001
NEGATIVE

Figure 2.8. Time since the last regeneration event at each site across the annual precipitation gradient. On the basis of results reported in Chapter 3 it is assumed here that regeneration events are dependent on wildfire.

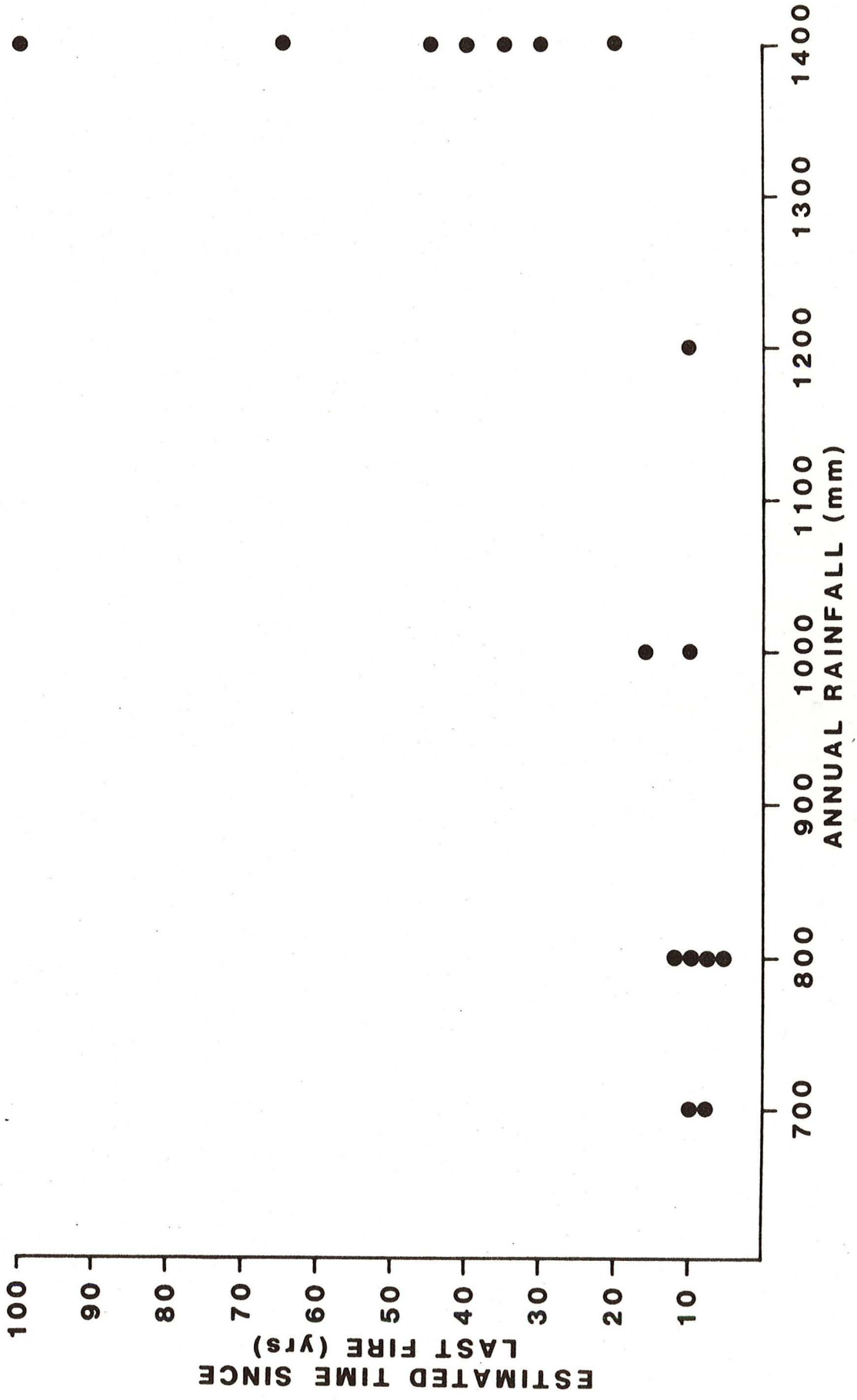

ESTIMATED TIME SINCE LAST FIRE (yrs)
100
90
80
70
60
50
40
30
20
10
700
800
900
1000
1100
1200
1300
1400
ANNUAL RAINFALL (mm)

Figure 2.9. Relationship between ordination score of understorey and ground covers and estimated time since the last fire ($r=0.81$ $P<0.05$) for seven high annual rainfall stands (>1400mm).

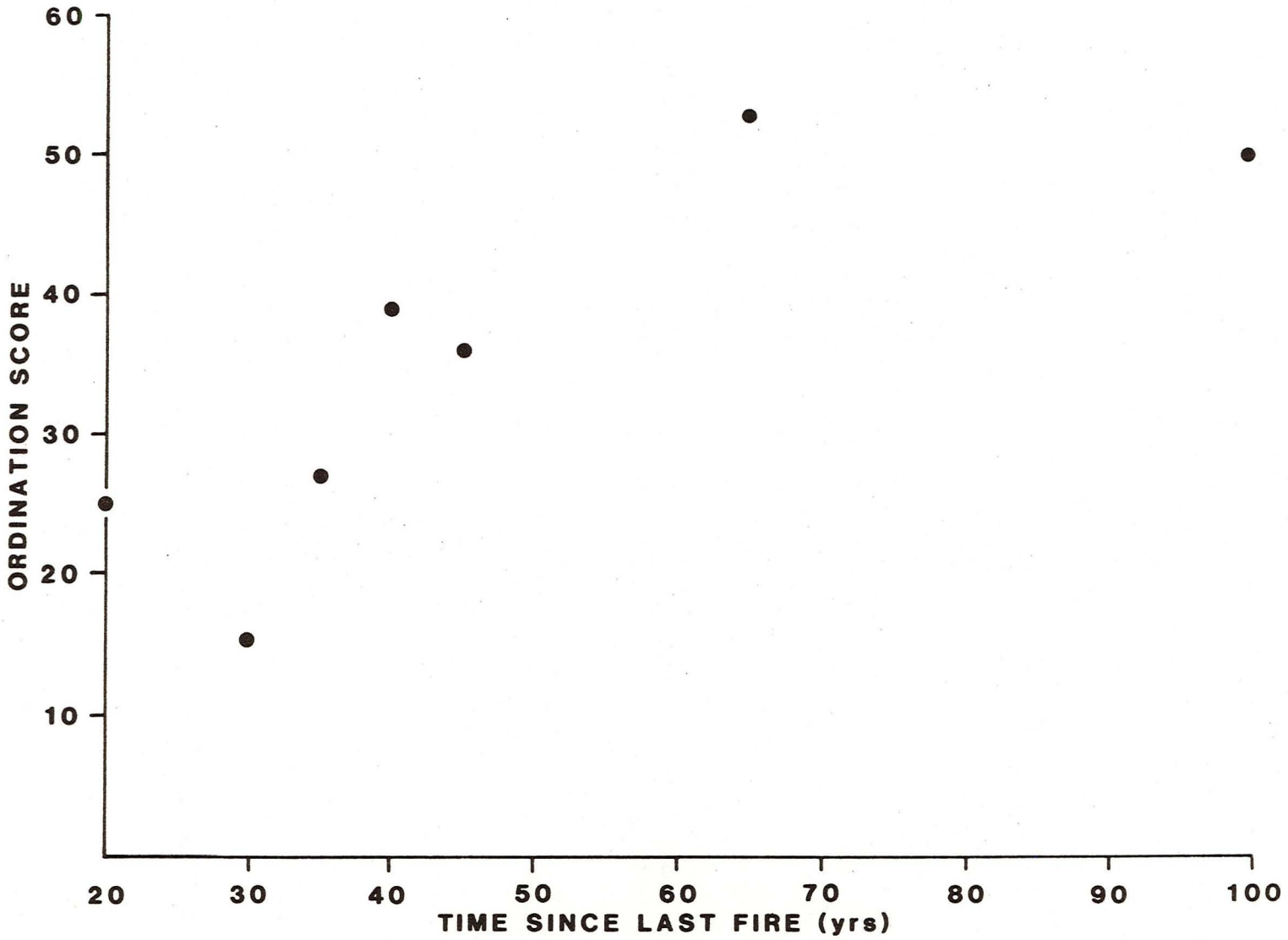
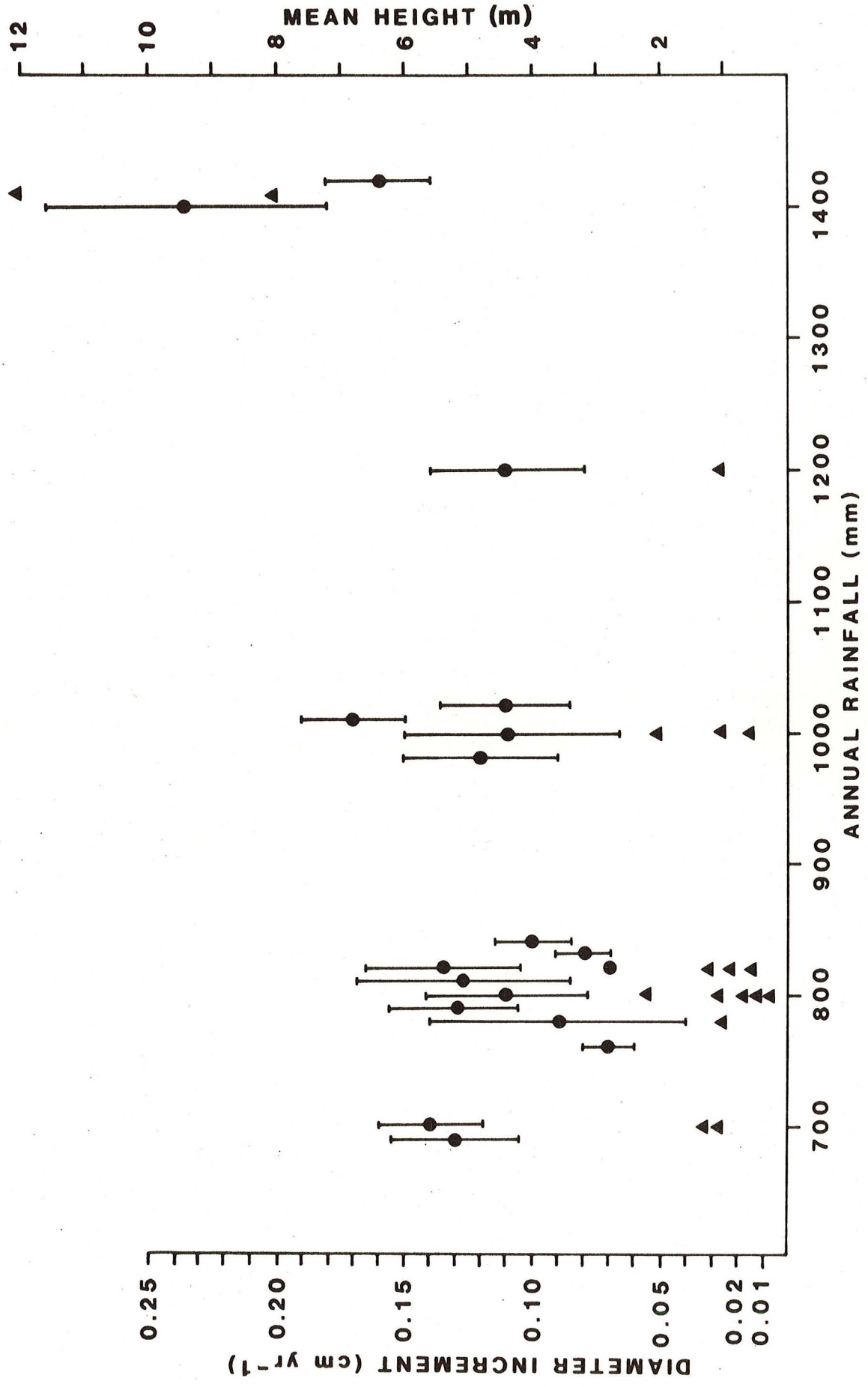

60
50
40
30
20
10
ORDINATION SCORE
20
30
40
50
60
70
80
90
100
TIME SINCE LAST FIRE (yrs)

Figure 2.10. Mean and 95% confidence interval of mean annual sapling stem base diameter increment and mean estimated height of saplings (▲) for each site across the annual precipitation gradient.


MEAN HEIGHT (m)
12
10
8
6
4
2
ANNUAL RAINFALL (mm)
700
800
900
1000
1100
1200
1300
1400
DIAMETER INCREMENT (cm yr⁻¹)
0.25
0.20
0.15
0.10
0.05
0.02
0.01

of the next fire (Figure 2.10), as well as controlling the number of days suitable for wildfire.

## 2.5 DISCUSSION

Eucalypts are not regarded as suitable species for detailed dendrochronological studies (Ogden, 1978; Dunwiddie and LaMarche, 1980), although they are known to have considerable dendroecological potential (Gilbert, 1959; Morrow and LaMarche, 1978; Mucha, 1979; Banks, 1982). The distinct annual growth rings formed by *E. delegatensis* have been studied to explore fire history (Costin, 1954), past insect defoliations (Mazanec, 1968; Readshaw and Mazanec, 1969) as well as the effect of intraspecific competition in multi-aged stands (Goodwin, 1984). *E. delegatensis* is highly suitable for dendrodemographical studies because it is non-lignotuberous and therefore stem age and tree age are the same. However, most studies of eucalypt tree age rest on the assumption of annual growth ring formation. The clearing of *E. delegatensis* plantations of known age would provide an opportunity to test this assumption. In this study analysis was restricted to 10 year age classes in light of this assumption and other possible sources of error (p. 16).

The demographic structures found in the *E. delegatensis* tall open forests with closed broad-leaf shrub or rainforest understoreys (sites 1-7, Figure 2.1) are widely at variance with those found in the forests dominated by other eucalypts lacking the lignotuberous means of recovery from fire. The characteristic pattern for these forests is recorded and

theorized to be virtually complete even-agedness (Felton, 1976; Cremer et al., 1978; Mount, 1979; Ashton, 1981). The assumption of even-agedness in these wet ash forests relies on the sensitivity of the non-lignotuberous eucalypts to fire, and is undoubtedly correct for the large areas of Eucalyptus regnans forest that have regenerated after major conflagrations (e.g. Ashton, 1976). Nevertheless, the literature records several examples of burning in E. regnans stands which failed to kill the eucalypts while temporarily destroying the dense understorey (Cremer, 1962; Ashton, 1956, 1981), and E. regnans stands containing trees of widely different size classes can be observed in the Mt. Field National Park and elsewhere in Tasmania. E. delegatensis is less susceptible to firekill than is E. regnans, making it much more likely that a fire will kill few or no trees and will also result in recruitment. The success of the newly recruited seedlings will ultimately depend on the competition for resources provided by the surviving mature trees. Stand 7 provides an example of a situation in which only a few individuals that established after the last fire have been recruited into the overstorey, most having remained suppressed in the understorey (Figure 2.2 and Table 2.4).

It is possible that the demographic structure of stands such as 11, 21 and 23 has developed as a result of a change of firing pattern with the extermination of the Tasmanian hunters and gatherers. These stands may have been maintained as woodland by frequent aboriginal firing; the decline of the aboriginals having led to a fire free period, eventually followed by one or several

Plate 2.5. Woodland form E. delegatensis tree with adjacent dense regrowth on the basaltic western slopes of the Ouse River, near Waddamana.

severe conflagrations. This hypothesis is supported by the long history of aboriginal occupation of the Tasmanian uplands (Cosgrove, 1983), the documented rainforest invasion of E. delegatensis forest in high rainfall areas (Needham, 1960; Ellis 1964; Orme, 1971), the presence of old E. delegatensis trees of savannah form intermixed with dense and upright regrowth (Plate 2.5) and the restriction of these major age class peaks to the last 160 years (Figure 2.2). A similar transition has occurred in the Australian mainland E. delegatensis forests (Flood, 1980; Costin, 1954) where it has been suggested that the woodlands were the climax community (Costin, 1954; Park, 1976; Shughart and Noble, 1981). In Kosciusko in particular , frequent firing by aboriginals may have eliminated some of the species, such as Nothofagus cunninghamii, which could grow (Costin and Polach, 1970) and has (Caine and Jennings, 1968) grown in the area, and which is capable of displacing E. delegatensis elsewhere. The increased incidence of fire scars in stem sections of old trees since European settlement (Costin, 1954; Banks, 1982) indicates a shift towards increased severity but far from proves a climax status for E. delegatensis woodland.

The multi-modal distribution of tree age and the suppressed layer of even-aged regeneration suggests that fire is critical in the natural regeneration of dry open E. delegatensis forests. The regeneration dynamics of this forest type are documented in the following three chapters.

# CHAPTER THREE

## THE POPULATION DYNAMICS OF MULTI-AGED E. DELEGATENSIS FORESTS.

### 3.1 INTRODUCTION

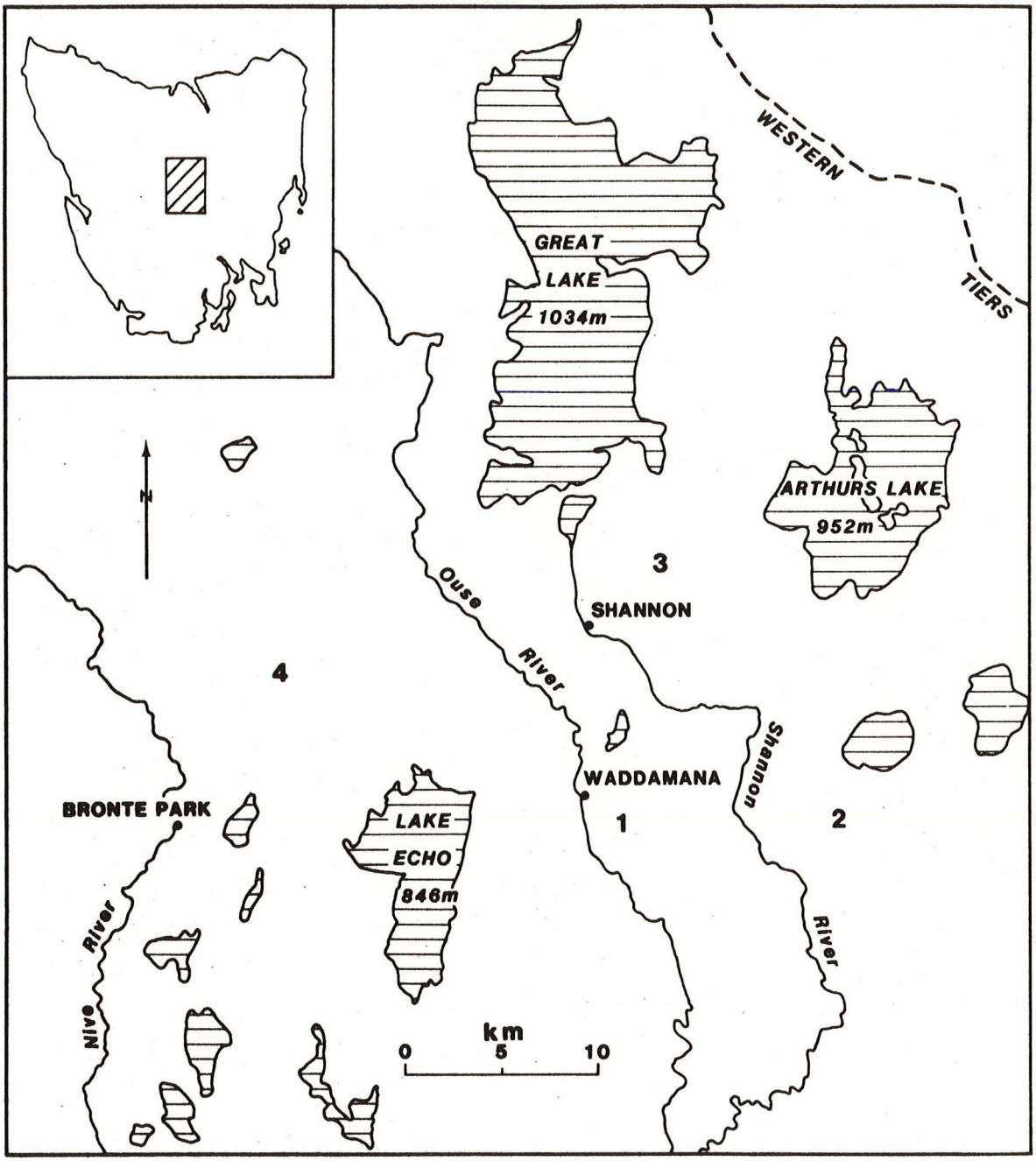
The natural regeneration processes of dry multi-aged eucalypt forests are poorly understood. The results of the demographic structure study showed that "dry" (< 1300 mm annual rainfall), frequently burnt E. delegatensis forests on dolerite had phasic overstorey recruitment and that the size of any cohort was extremely variable. The survey also showed that the characteristic layer (c.1 m) of slow growing E. delegatensis advance growth in the dry forests was largely even-aged (Table 2.4).

The aim of this chapter is to document the effect of recent fires in E. delegatensis forests on the overstorey trees and the understorey advance growth, and to determine what factors control the successful establishment of seedlings in multi-aged E. delegatensis forests.

### 3.2 METHODS

The response of E. delegatensis forests on dolerite to fires of varying intensity was studied at three different locations on the Central Plateau (Figure 3.1). At the Serpentine River (site 4) an area of forest was severely burnt by an illegally lit wildfire which nearly destroyed the township of Bronte Park in February 1982 (Figure 3.1, site 17 in Chapter 2). Eight months after the fire a 1000 m line transect was run across a mildly burnt flank of the burnt area and a second transect was placed in

Figure 3.1. Location of study sites on the Central Plateau, Tasmania. 1 = Waddamana Research Site , 2 = Bakers Tier, 3 = Pensford , 4 = Serpentine River .


WESTERN
TIERS
GREAT
LAKE
1034m
ARTHURS LAKE
952m
N
3
SHANNON
Ouse
River
4
WADDAMANA
Shannon
River
BRONTE PARK
LAKE
ECHO
846m
1
2
River
Nive
km
0
5
10

an unburnt forest on the same slope with similar understorey vegetation. One $m^2$ samples were taken at 10 m intervals to assess the density of germinates. The level of fire damage to the overwood was assessed in the burnt area.

One and a half years after the fire the level of recovery of the overwood in the more severely burnt area at Serpentine River was determined by randomly selecting trees (> 10 cm diameter at breast height over bark) and classifying them as either undamaged, fully covered in epicormics, lower half of trunk covered in epicormics, dead but standing,or fallen. The density of advance growth (< 10 cm d.b.h.o.b.) and germinates was found by running 2 m wide belt transects through the severely burnt stand. The advance growth was classified as either dead, undamaged or resprouted from the base. The heights of the resprouts and germinates were measured for randomly selected individuals intercepted on line transects. The presence or absence of butt damage was recorded for 72 trees. Where stems had butt damage the presence or absence of dead limbs near the tree was noted.

An area of forest considered typical of E. delegatensis on the eastern Central Plateau was selected at Bakers Tier (Figure 3.1, site 2) where five 20 m transects were laid out in parallel 10 m apart. On each transect ten permanent one $m^2$ quadrats were established and the height and the coordinates of all observed advance growth were recorded. On 18/11/1981 in the late afternoon the area was burnt in a cool fire lit by the Tasmanian Forestry

Commission. The plots were then scored for the proportion of their area burnt. Nine months later the fate of the advance growth was determined and the height of the surviving plants or the resprouts was recorded for plots that had at least 5% of their area burnt.

Following a heavy sawlogging operation on private property near Pensford (Figure 3.1, site 3) the cutover stand was severely burnt in November 1981, by a fire which escaped into an adjacent unlogged E. gunnii forest . Twenty one months after the fire, previously healthy dense groups of saplings (> 1 m) which occur in gaps were assessed as being either dead, undamaged or recovering by basal resprouts. The height of plants intercepted on line transects from each category was measured to test the hypothesis that taller plants are more likely either to resprout or to survive wildfire undamaged.

At the Waddamana research site (Figure 3.1, site 1,site 18 in Chapter 2) the relationship between height, diameter and bark thickness was determined by measuring plants cut down at ground level. The plants were located on line transects run from beneath forests across dense stands of healthy regrowth (< 10 cm d.b.h.o.b.) growing in gaps.

At Waddamana the following experiment was established to measure the combined effect of three different types of unburnt seedbed and three different levels of canopy on the establishment of E. delegatensis germinates. Nine randomly located plots were

marked out in adjacent and originally environmentally similar forests which had been subjected to three overwood treatments ; viz 100%, 50% , 0% canopy removal (=clearfell, shelterwood and forest). Each plot consisted of three 1 $m^2$ quadrats; the first was heavily dug with a mattock, the second was scalped to remove all the above ground biomass and the third was left untreated. On the 29/5/1982 one half of each quadrat was sown with 6.2 g of seed and chaff which had been collected from the locality. During sowing the unsown half of the quadrat was covered with a plastic sheet. The number of germinates and their growth was recorded over the summer of 1982/83. On the 11/1/1983 the ground cover of the mechanically disturbed quadrats was assessed. As no fences were employed in the study, the effect of browsing was indirectly estimated by counting the number of animal scats in 50 one $m^2$ quadrats placed in each canopy treatment. The % cover of machine-caused soil disturbance was visually estimated in 100 one $m^2$ randomly placed quadrats in the clearfelled area.

## 3.3 RESULTS

### 3.3.1 Damage to trees.

The ground fire at the flank of the area burnt at Serpentine River (site 4) caused only isolated cases of crown scorch to the overstorey. In the nearby severely burnt forest no crown escaped undamaged.For this stand Table 3.1 shows that 77% of the trees recovered and only 6% were killed. Of those killed 22% were destroyed by stem failure and all these were greater than 40 cm in diameter, while 67% died standing and all were in the smaller size classes. Mechanical failure is the end result of recurrent

TABLE 3.1

Recovery of trees 18 months after a high intensity fire at Serpentine River.

| Size Class | Undamaged | | Full resprout | | Lower half resprout | | Killed, standing | | Killed, fallen | | Total |
|---|---|---|---|---|---|---|---|---|---|---|---|
| d.b.h. (cm) | n | % | n | % | n | % | n | % | n | % | |
| 10 - 40 | 0 | 0 | 53 | 70 | 17 | 22 | 6 | 8 | 0 | 0 | 76 |
| >40 | 0 | 0 | 53 | 87 | 5 | 8 | 1 | 2 | 2 | 3 | 61 |
| TOTAL | 0 | 0 | 106 | 77 | 22 | 16 | 7 | 5 | 2 | 1 | 137 |

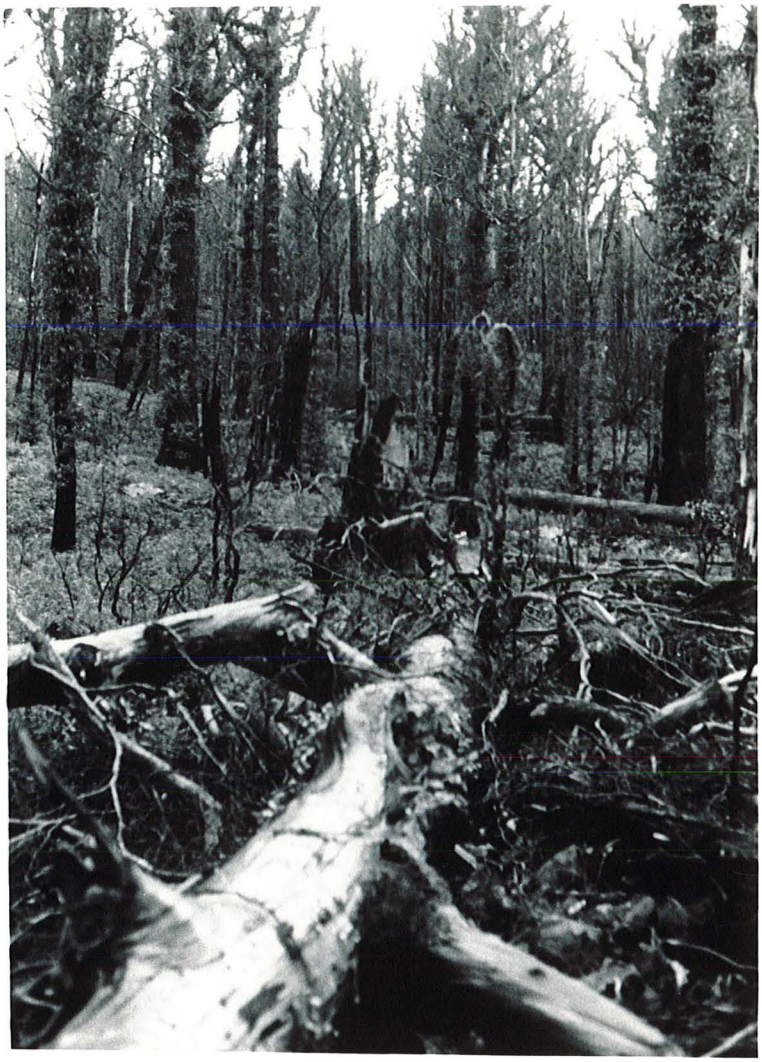
TABLE 3.2

The occurrence of *E. delegatensis* butt damage[1] at Serpentine River.

| Size Class | Undamaged | | Damaged | | Total |
|---|---|---|---|---|---|
| d.b.h. (cm) | n | % | n | % | |
| 10 - 40 | 10 | 43 | 13 | 57 | 23 |
| > 40 | 15 | 31 | 34 | 69 | 49 |
| TOTAL | 25 | 35 | 47 | 65 | 72 |

1. Butt damage was subjectively defined as the destruction of the cambium and the attrition of the stem wood.

Plate 3.1. Mechanical failure of a repeatedly butt damaged stem in the severely burnt area at Serpentine River. Note the epicormic recovery of the defoliated trees in the background.



fire damage to the tree butt (Plate 3.1). Such butt damage is common in the forest (Table 3.2) and is related to the presence of large fuel accumulations near the base of the tree (Table 3.3).

### 3.3.2 Damage to advance growth.

Advance growth is easily killed by fire (Table 3.4). Following the high intensity fire at the Serpentine River (site 4) only 5% of the advance growth resprouted and these plants were taller than the fire killed advance growth (killed $\bar{x}$ 175 range 50-500 cm : resprouts $\bar{x}$ 290 range 75-600 n=4). This trend is further borne out by the study at Pensford (site 3) where fire killed plants were significantly smaller than resprouting plants ($p<0.01$) and the latter were significantly smaller than the surviving advance growth ($p<0.001$). The high density of tall regrowth found in this area accounts for the increased proportion of both resprouting and surviving stems (Table 3.5).

Bark thickness, under bark stem diameter, and height are all highly linearly intercorrelated ($p<0.001$) for plants which are the same age. The marked increase in bark thickness with height (Figure 3.2) is due to the development of a rough fibrous bark which replaces the smooth thin bark at the base of the taller stems. The thicker bark appears to give protection to the cambium of the taller plants with undamaged crowns, and also protects the basal epicormic buds of the defoliated saplings.

### 3.3.3 The establishment of germinates.

Figure 3.2. Relationship between height and bark thickness for E. delegatensis saplings.

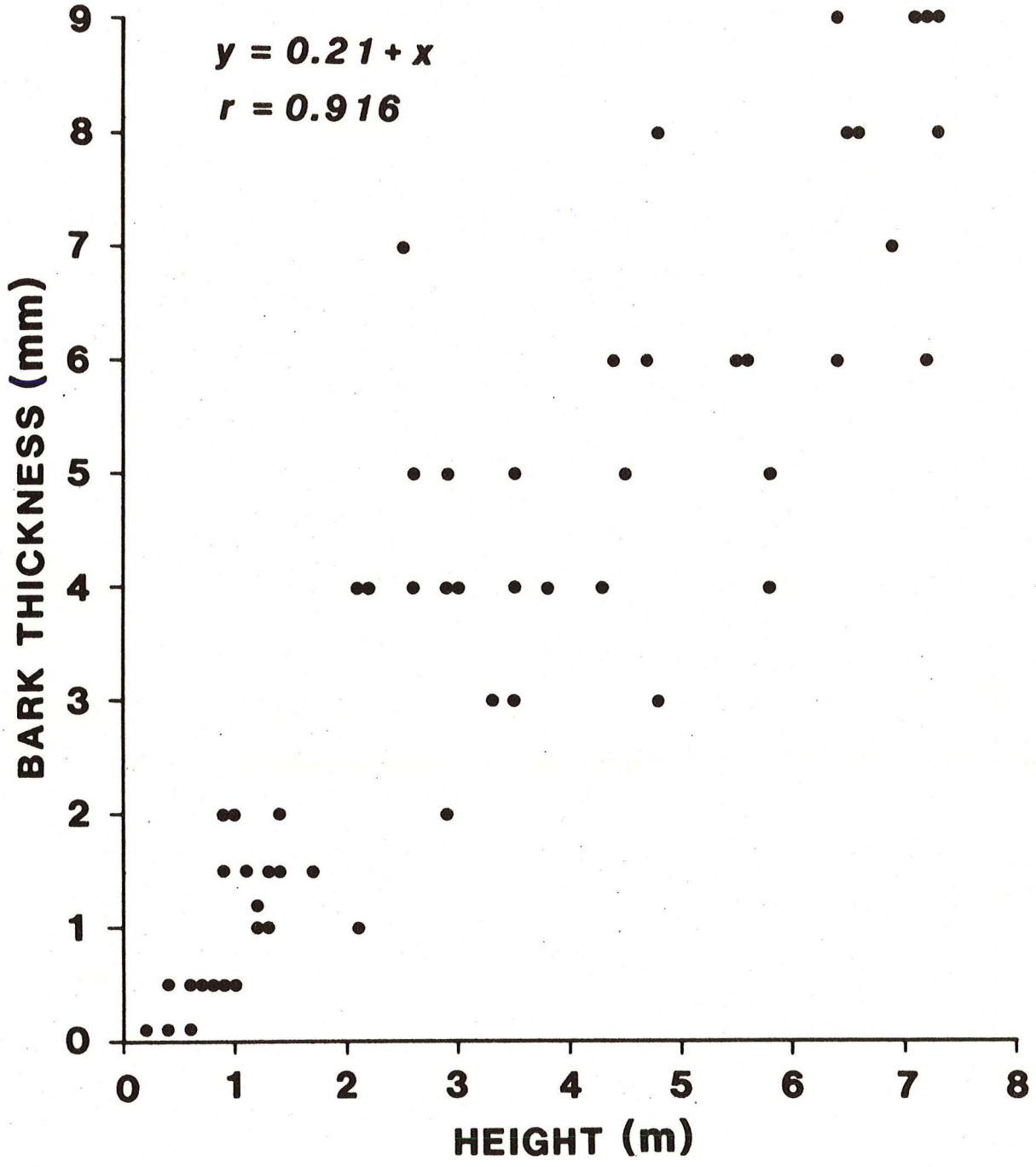

y = 0.21 + x
r = 0.916
BARK THICKNESS (mm)
HEIGHT (m)
0
1
2
3
4
5
6
7
8
9

TABLE 3.3

The occurrence of dead limbs (>10cm diameter) lying at the base of butt damaged stems.

| Size Class | No limbs at tree base | | With limbs at tree base | | Total |
|---|---|---|---|---|---|
| d.b.h. (cm) | n | % | n | % | |
| 10 - 40 | 2 | 15 | 11 | 85 | 13 |
| > 40 | 8 | 24 | 26 | 76 | 34 |
| TOTAL | 10 | 21 | 37 | 79 | 47 |

TABLE 3.4

The frequency of killed, resprouted and undamaged *E. delegatensis* regeneration following a low intensity fire at Bakers Tier and a high intensity fire at Serpentine River.

| | Height class | Killed | | Resprouted | | Undamaged | | Total |
|---|---|---|---|---|---|---|---|---|
| Site | (cm) | n | % | n | % | n | % | |
| Serpentine River | >50 | 53 | 95 | 3 | 5 | 0 | 0 | 56 |
| Bakers Tier | > 2 | 87 | 94 | 4 | 4 | 2 | 2 | 93 |
| | < 2 | 99 | 100 | 0 | 0 | 0 | 0 | 99 |
| TOTAL | | 186 | 97 | 4 | 2 | 2 | 1 | 192 |

TABLE 3.5

Frequency of three classes of fire damaged saplings (>1m tall) following a severe burn in a heavily sawlogged *E. delegatensis* forest. The mean and standard error of stem height is shown for each class.

| | Resprout | | Killed | | Undamaged | | Total |
|---|---|---|---|---|---|---|---|
| | n | % | n | % | n | % | |
| Number | 63 | 43 | 64 | 43 | 20 | 14 | 147 |
| | $\bar{x}$ | SE | $\bar{x}$ | SE | $\bar{x}$ | SE | - |
| Height | 5.2 | 0.3 | 4.0 | 0.3 | 10.1 | 0.4 | - |

TABLE 3.6

Density of germinates and advance growth at three sites following different intervals since burning.

| | Site | Type of fire | Time since last fire (mths) | $\bar{x}$ density $m^{-2}$ | No. of plots |
|---|---|---|---|---|---|
| Germinates (<2cm) | Bakers Tier | unburnt | ? | 2.4 | 50 |
| | | mild | 9 | 0.3 | 30 |
| | | mild | 15 | 0 | 30 |
| | Serpentine River | none | ? | 0 | 100 |
| | | mild | 8 | 0.4 | 100 |
| | | mild | 18 | 0.002 | 800 |
| | | severe | 18 | 0.015 | 1000 |
| Advance growth (>2cm) | Bakers Tier | unburnt | ? | 2.4 | 50 |
| | Serpentine River | unburnt | ? | 0.032 | 760 |

No germinates were found in the unburnt forest at Serpentine River (site 4) while many were found in the adjacent mildly burnt area. Eight months after the fire there were 4000 germinates per ha. Only twenty germinates per ha were alive 18 months later when there were 150 germinates per ha in the severely burnt forest. The cool fire at Bakers Tier (site 2) produced one germinate on the 30 burnt quadrats and this plant died over the subsequent summer. Table 3.6 shows that the prefire density of advance growth is greater than the number of germinates that established after the various fires. The height growth of germinates is the same as the height growth of the basal resprouts from fire truncated advance growth. Surprisingly the resprout recovery of fire truncated, subdominant E. dalrympleana is significantly greater ($p<0.001$) than that of E. delegatensis (Table 3.7). The Bakers Tier (site 2) data showed that seeds can germinate on the forest floor in the absence of fire.

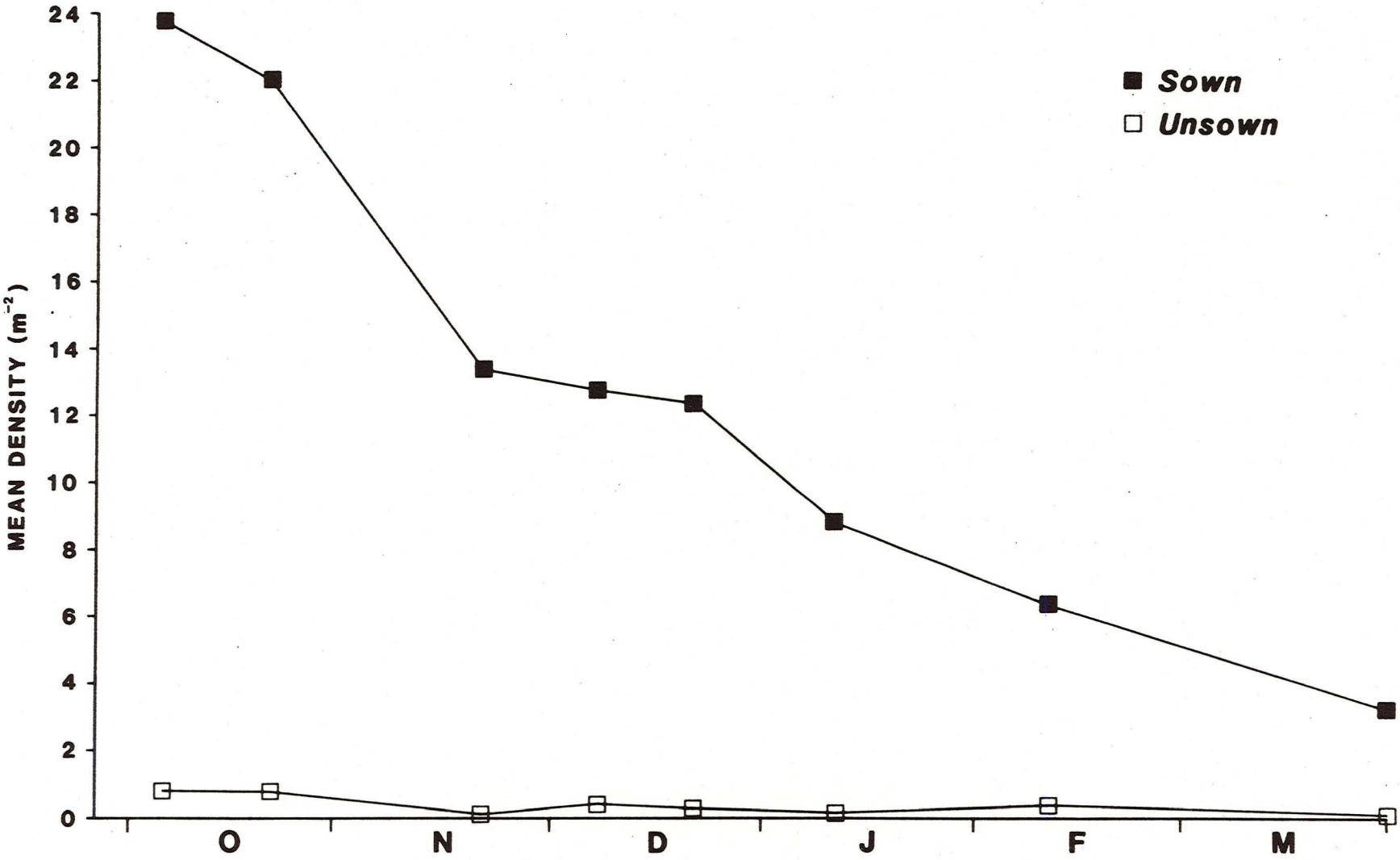
In the experiment at Waddamana (site 1) the amount of natural seed input on the various treatments was assessed by finding the number of germinates on the unsown halves of the quadrats. The mean germination on the unsown half of the quadrats was significantly less ($P<0.001$) than the mean number of germinates on the sown half of the quadrats (Figure 3.3). To remove the effect of natural seed input, the number of germinates on the unsown half of the quadrat was subtracted from the sown half for all treatments and all dates of sampling. Analysis of variance of the adjusted densities showed that there was no

TABLE 3.7

Height growth of basal resprouts and germinates following a severe fire at Serpentine River.

| Type | Mean height (cm) | SE | n |
|---|---|---|---|
| *E.delegatensis* germinates | 8.6 | 1.8 | 15 |
| *E.delegatensis* resprouts | 12 | 4.8 | 4 |
| *E.dalrympleana* resprouts | 53 | 7.0 | 11 |

Figure 3.3. Mean densities of sown and natural germinates pooled for all treatments from October 1982 until March 1983.


MEAN DENSITY ($m^{-2}$)
24
22
20
18
16
14
12
10
8
6
4
2
0
O
N
D
J
F
M
Sown
Unsown

interaction between the canopy and seedbed treatments, but that the canopy and seedbed treatments did have a significant effect on the germinates. There was also a significant effect of canopy and seedbed treatment on the ground cover.

Figure 3.4 shows that the mean number of germinates on the uncultivated seedbeds was significantly lower than on the other two seedbed treatments. Figure 3.5 shows that, at the first sampling, the clearfelled uncultivated seedbed treatment had a significantly ($P<0.05$) higher mean stocking than the uncultivated seedbeds beneath the other two canopy treatments. Although not significant,this trend is apparent for the other sampling dates. The higher mean density of germinates on the "uncultivated" seedbeds in the clearfelled area is probably related to soil disturbance during logging (area of bare ground : clearfell $\bar{x}$ 13% SE 2.8 , unlogged 0.0 %). Heavy soil disturbance produced more germinates than did scalping, a trend which is statistically significant for five of the eight samplings (Figure 3.4). Germinates were found to be significantly ($P<0.001$) associated with small niches in the seedbed, and mattocking was found to produce the greatest number of such micro habitats. Furthermore, heavy soil disturbance was found to destroy rootstocks, thereby reducing the amount of ground cover regeneration. Figure 3.6 shows that six months after the seedbed preparation, the mattocked treatment had more bare ground ($P<0.001$) than the scalped treatment, while the latter had significantly ($P<0.05$) more cover of resprouting woody species and grass. The removal of ground cover vegetation competition

Figure 3.4. Mean adjusted pooled densities of germinates for each seedbed type over the summer of 1982/83. Vertical lines indicate similar ($P<0.05$) means as determined by Student-Newman-Keuls range test.

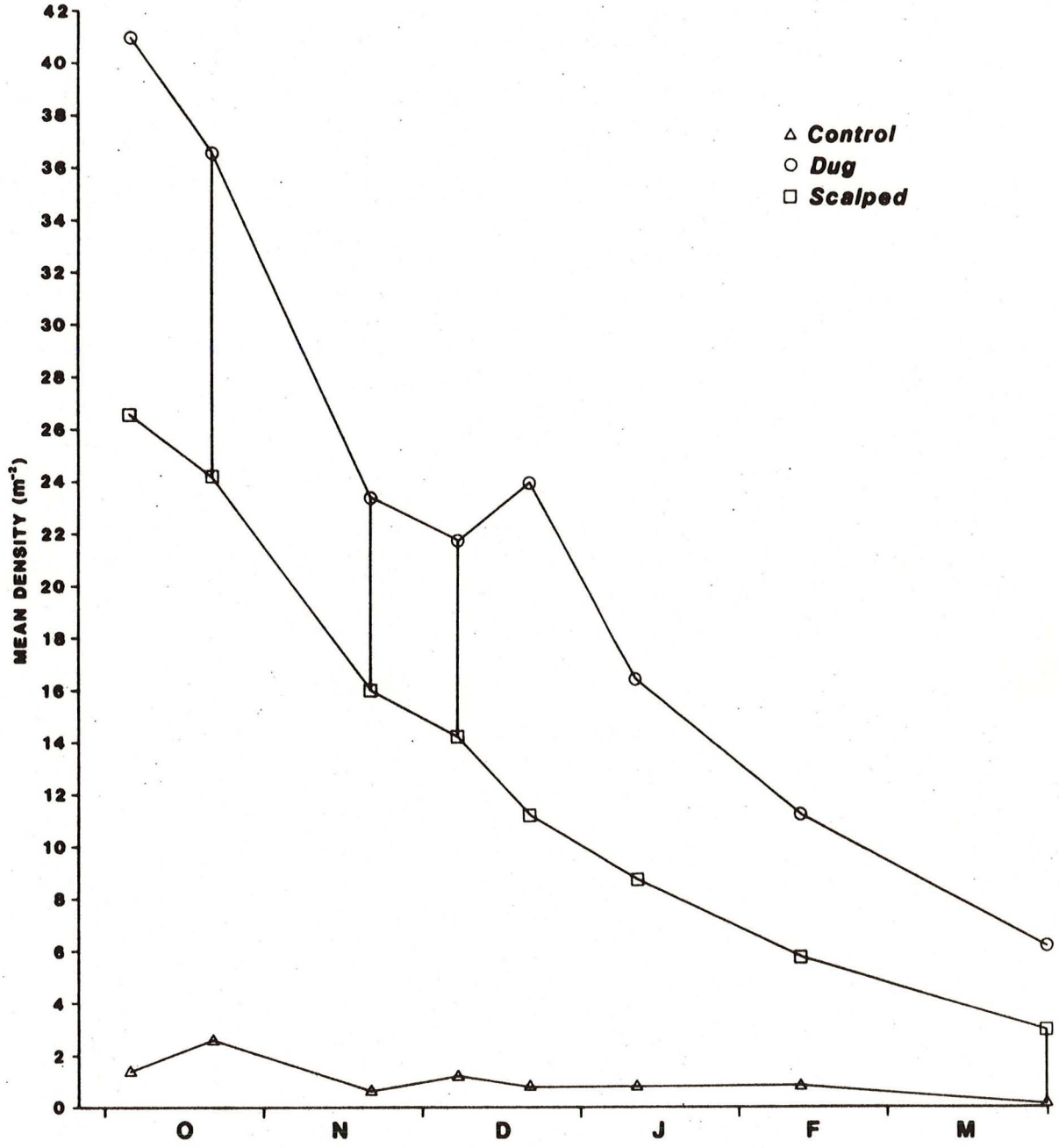

MEAN DENSITY ($m^{-2}$)
42
40
38
36
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
O
N
D
J
F
M
Control
Dug
Scalped

Figure 3.5. Mean adjusted pooled densities of germinates on uncultivated seedbeds beneath three different canopy treatments over the summer of 1982/83. Vertical lines indicate similar ($P<0.05$) means as determined by Student-Newman-Keuls range test .

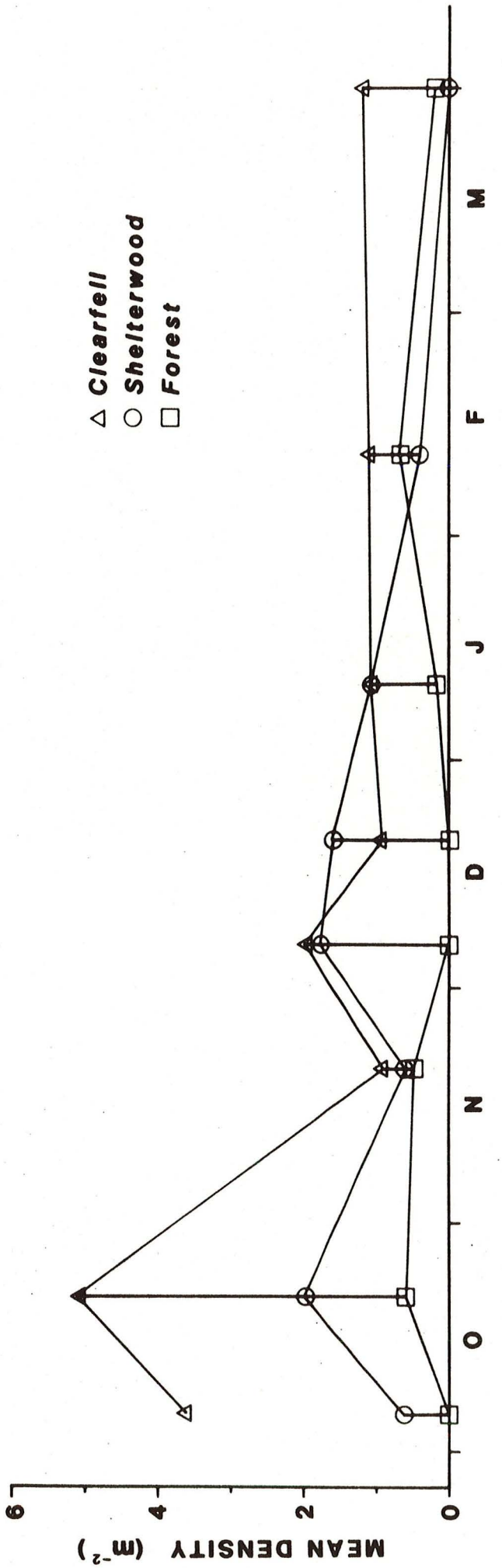

Clearfell
Shelterwood
Forest
MEAN DENSITY (m⁻²)
0
2
4
6
O
N
D
J
F
M

Figure 3.6. Number of animal scats and mean percentage ground cover beneath the three canopy treatments and on the cultivated seedbeds six months after the soil disturbance.Solid horizontal lines denote statistically similar ($P<0.05$) means as determined by Student-Newman-Keuls range test.Dotted lines indicate that clearfell and forest treatments have means that are statistically similar,but different to the shelterwood mean. Stars indicate significantly different ground cover on the two cultivated seedbeds as determined by oneway analysis of variance.

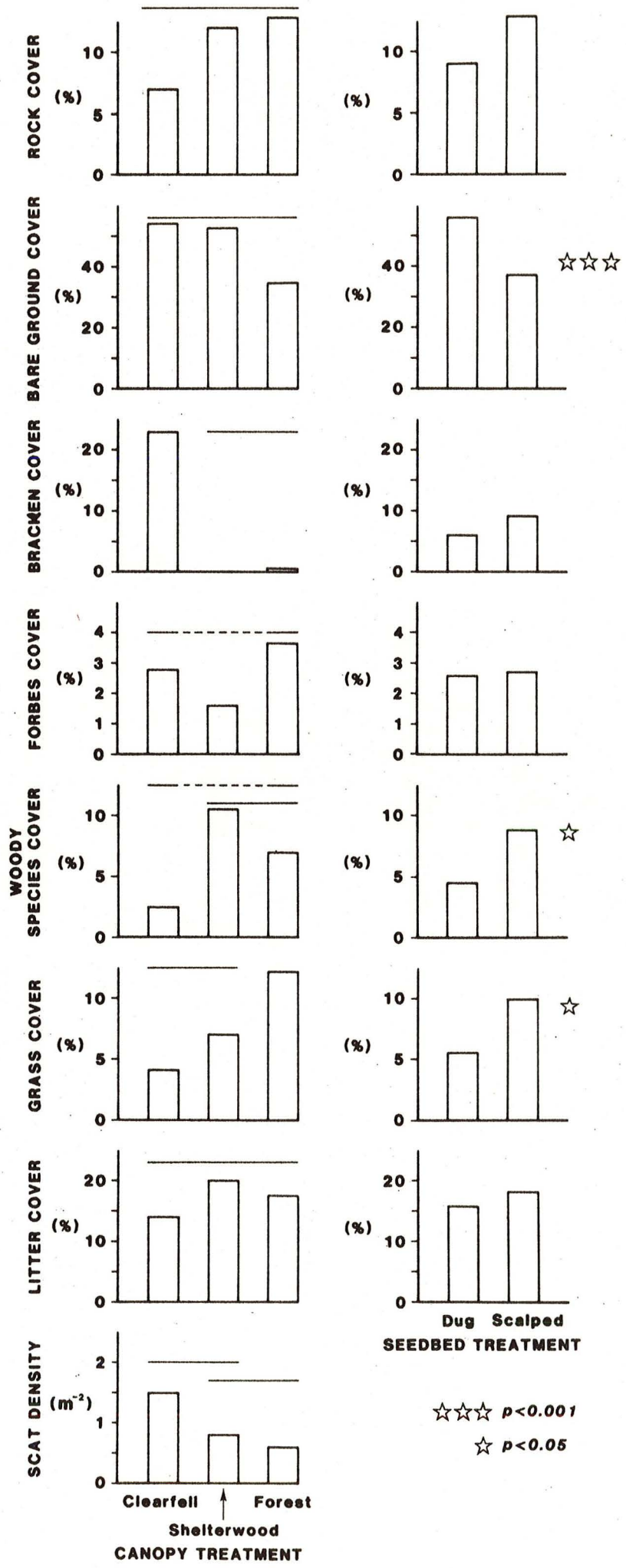

ROCK COVER
BARE GROUND COVER
BRACKEN COVER
FORBES COVER
WOODY SPECIES COVER
GRASS COVER
LITTER COVER
SCAT DENSITY
(%)
(m⁻²)
☆☆☆
☆
Clearfell
Forest
Shelterwood
CANOPY TREATMENT
Dug
Scalped
SEEDBED TREATMENT
☆☆☆ p<0.001
☆ p<0.05

Figure 3.7. Mean adjusted densities of germinates pooled for the three canopy treatments over the summer of 1982/83. Verticle lines link similar ($P<0.05$) means as determined by Student-Newman-Keuls range test. The amount of rain that fell between sampling dates is also shown.

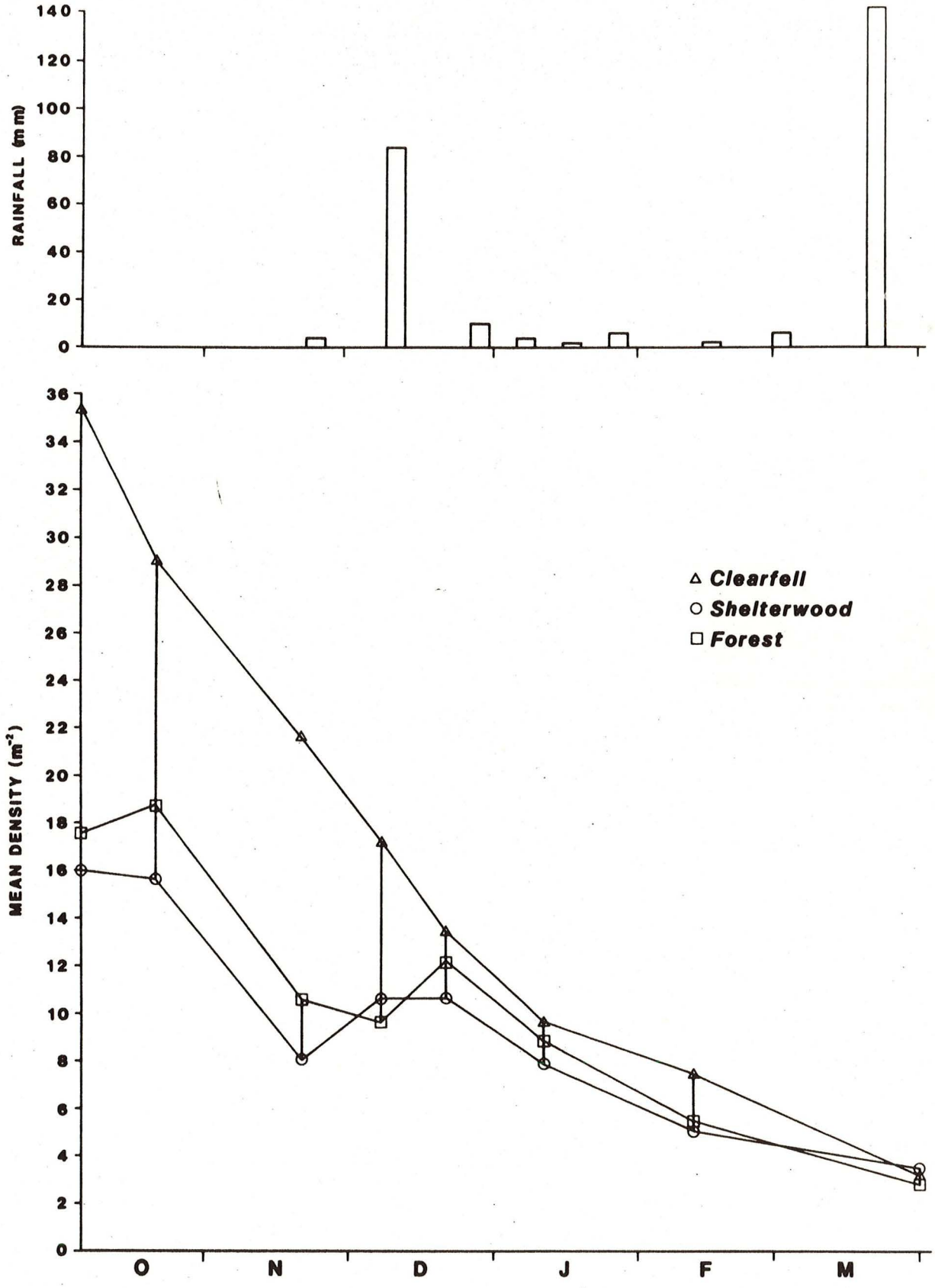
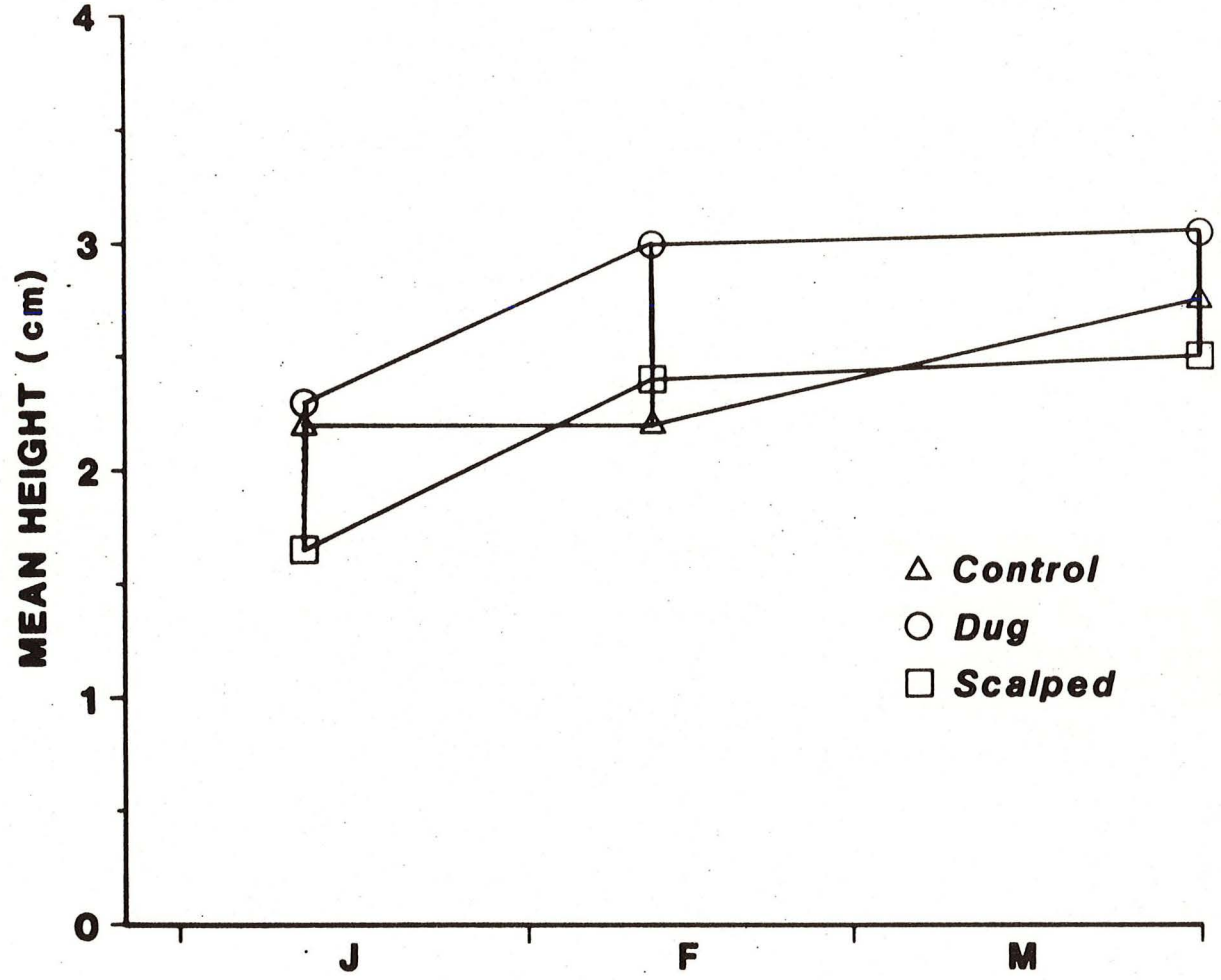

RAINFALL (mm)
140
120
100
80
60
40
20
0
MEAN DENSITY (m⁻²)
36
34
32
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
0
O
N
D
J
F
M
△ Clearfell
○ Shelterwood
□ Forest

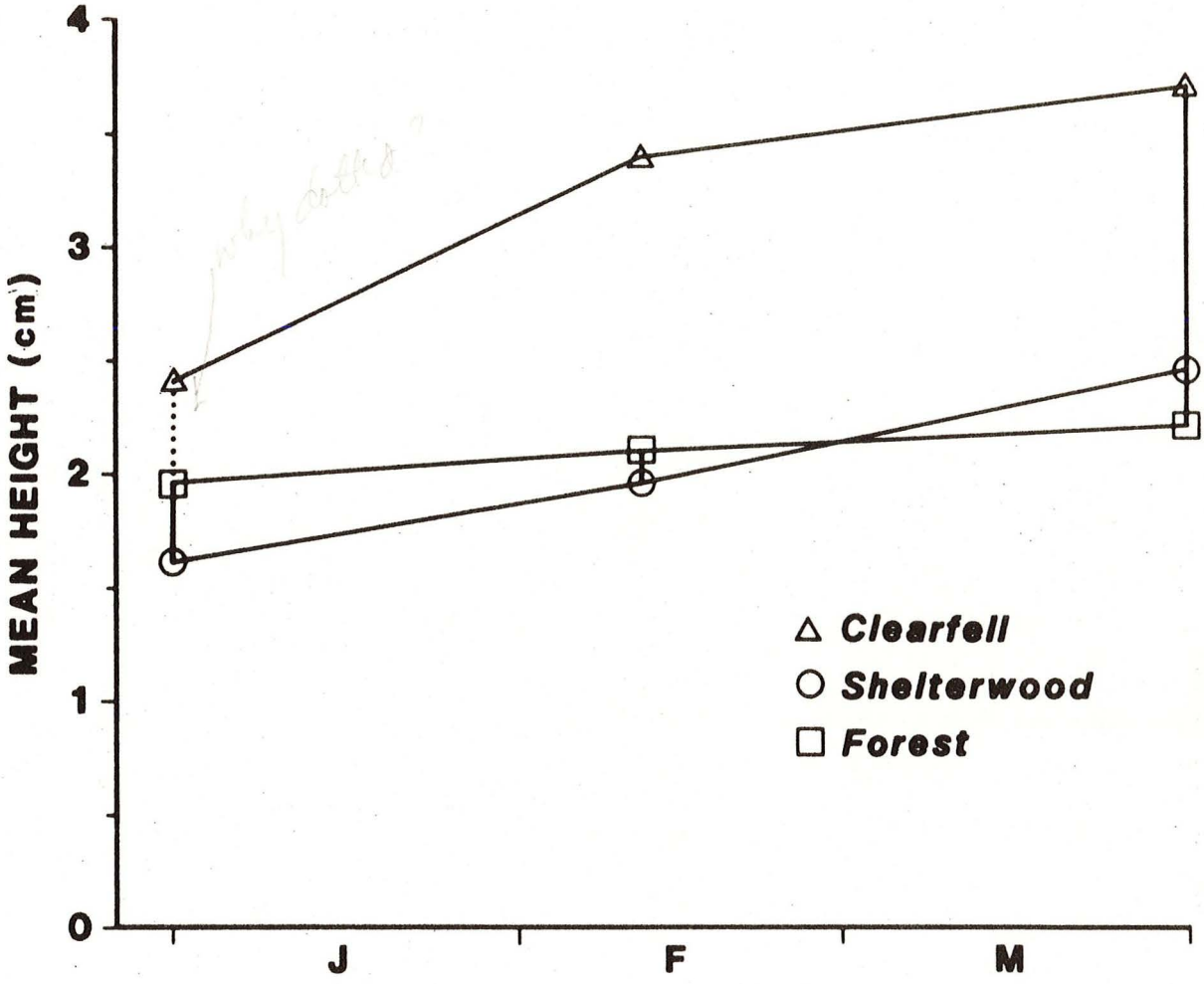
Figure 3.8. Mean height of tallest germinates pooled for each seedbed treatment over the summer of 1982/83. Vertical lines link similar ($P<0.05$) means as shown by SNK range test .


MEAN HEIGHT (cm)
4
3
2
1
0
J
F
M
Control
Dug
Scalped

may have contributed to the greater, albeit not significant, height growth of the germinates on the mattocked seedbeds (Figure 3.8). The lack of soil niches and the effect of ground cover competition may have contributed to the failure of any germinate to establish on the uncultivated seedbed in the forest, although the effect of canopy is also critical to the establishment of the seedlings.

Full and partial canopy cover had statistically similar mean germinate densities throughout the time of sampling. The complete removal of the canopy produced higher mean densities for the first four dates of sampling, where the first and third were statistically different from the two other treatments. The increased mean density of germinates for the 100% and 50% canopy treatments in December may reflect the effect of heavy rain which fell in that month (Figure 3.7). Similarly,the dry summer may account for the mortality of germinates and the convergence of germinate densities for all treatments at the end of the summer. However, animal browsing may also be an important cause of germinate death (Figure 3.6) as the nipped stems of germinates were often observed. The presence of overwood had a significant suppressive effect upon the height of the tallest germinates (Figure 3.9) and also on the cover of bracken on the heavily disturbed seedbeds (Figure 3.6).

Figure 3.9. Mean height of tallest germinates pooled for each canopy treatment over the summer of 1982/83. Vertical and dotted lines link similar ($P<0.05$) means as determined by Student-Newman-Keuls range test .


MEAN HEIGHT (cm)
4
3
2
1
0
J
F
M
Clearfell
Shelterwood
Forest

## 3.4 DISCUSSION

The findings of the demographic survey indicated that the trees in dry *E. delegatensis* forest are fire resistant but that the understorey saplings are extremely fire sensitive. These conclusions are supported by the results of the studies of recently burnt *E. delegatensis* forests. The strong overwood recovery of these forests is similar to the response of other dry eucalypt forests following burning (Purdie and Slatyer, 1976; Christensen et al., 1981). Stem death is infrequent and, in the case of large trees, is caused by stem failure following recurrent fire damage to the butt. Jacobs (1955), Vines (1968) and Mount (1979) suggest that the combustion of accumulated fuel near the stem base is a significant cause of butt damage, and this appears to be the case with the frequently burnt stand at Serpentine River. The effect of flame vortices is probably also important (Gill, 1974). The death of the upright smaller stems (< 40 cm d.b.h.o.b.) may be related to their thin bark which affords little protection for the cambium from lethal temperatures (Gill and Ashton, 1968; McArthur, 1968; Vines, 1968). Van Loon (1971) found a direct relationship between both bark thickness and height and the survival of *E. pilularis* advance growth following fire, and such a relationship appears to account for the high proportion of vigorously growing *E. delegatensis* advance growth (< 10 cm d.b.h.o.b.) which survive a fire. The poor recovery of the suppressed fire damaged *E. delegatensis* advance growth is in marked contrast to that of lignotuberous eucalypts like *E. dalrympleana* at Serpentine

River (Harris, 1956; Henry, 1961; Henry and Florence, 1966; White, 1971; Purdie and Slatyer, 1976; Schuster, 1980). Even the non-lignotuberous *E. pilularis* is more fire resistant than *E. delegatensis*. Curtin (1966) reports a survival rate of 53% following a prescribed burn and van Loon (1971) found that only 2.5% of the advance growth was killed by a severe wildfire which defoliated 97% of the saplings. He notes however, that about 30% of suppressed advancee growth was killed by low intensity controlled fires. Van ?Loon reports that the basal resprouts are epicormic buds which are protected from lethal temperatures by soil surrounding the base of the stem. Such subterranean epicormic buds account for most of the regeneration after fire of suppressed *E. delegatensis* regeneration.

Fire produces a suitable seedbed for the establishment of germinates to replace the last generation of even-aged advance growth. However, because of the robust nature of mature *E. delegatensis*, only the few germinates that become saplings could escape death in the next fire and have a chance of recruitment into the overstorey. The low densities of germinates recorded after the various fires indicate the impact of rainfall patterns in the first few years following the burn on the resultant density of advance growth. This fact may partially explain why the density of advance growth was found to be extremely variable at the sites sampled for the demographic survey (Chapter 2).

As reported for *E. delegatensis* on the Australian mainland (Grose, 1957) and for other species of eucalypt (Jacobs, 1955;

Harris, 1956; Gilbert, 1958; Cunningham, 1960; Floyd, 1962; Florence, 1964; Dexter, 1967; Christensen and Schuster, 1979; Annels, 1980), Tasmanian E. delegatensis readily establishes on a disturbed mineral seedbed in the absence of fire. However, when isolated from the mineral soil, the seeds which germinate are unable to establish (Grose, 1957). Given the very infrequent occurrence of disturbed soil in an unburnt forest and the even-aged nature of the advance growth the natural regeneration of E. delegatensis appears to be largely dependent upon fire. Furthermore, the few seedlings which do establish between fires would be suppressed by the canopy (Henry and Florence, 1966; Gill and Ashton, 1971; Schuster, 1980). This suppressive influence of the undamaged canopy is known to stunt both seedlings and saplings (Jacobs, 1955; Harris, 1956; van Noort, 1960; Henry and Florence, 1966; Gill and Ashton, 1971; Incoll, 1979a; Schuster, 1980; Ashton and Willis, 1982; Rotheram, 1983) but the cause has been considered problematical. The following chapter reports the results of studies into the suppression of E. delegatensis advance growth.

# CHAPTER FOUR

# EDAPHIC CONTROL OF THE RECRUITMENT OF E. DELEGATENSIS REGENERATION

## INTRODUCTION

The competitive influence of trees on understorey regeneration has been observed and measured in several different eucalypt forests (Henry and Florence, 1966; Gill and Ashton, 1971; Incoll, 1979a; Rotheram, 1983). However the nature of the competitive influence has not been explained. In multi-aged *E. delegatensis* forests there is evidence of intraspecific competition between mature and immature trees. The first section of this chapter documents this evidence while the latter sections report the results of experiments designed to identify the factors which are related to the suppressed growth of the understorey regeneration.

## 4.2 SUPPRESSION AND RELEASE OF E. DELEGATENSIS ADVANCE GROWTH

### 4.2.1 Introduction

A conspicuous feature of multi-aged *E. delegatensis* forests is the occurrence of dense, tall regrowth in forest gaps created by past selective logging. The competition gradient from forest to gap was intensively sampled at Waddamana (Figure 3.1) to find out which environmental factors were associated with the marked spatial variation in the productivity of the advance growth.

### 4.2.2 Methods

Two gaps with conspicuous regrowth in a flat area were bisected by a north-south line transect and the density, height and age of the tallest regeneration was recorded for each square metre along the traverse. The line was divided into 5 m x 2 m quadrats , in each of which the advance growth foliage and the top 10 cm of the mineral soil were randomly sampled, and typical leaf shape recorded. The foliage was air dried and ground into a 2 mm powder and subsampled for determination of the concentrations of N,P,K,Na,Ca, and Mg. The texture, pH and total and available concentrations of the above elements were also determined for the soil samples. Available nutrients were determined following extraction by Morgans reagent.For other methods see chapter two. A third gap on level ground was sampled by a north-south belt transect made up of 12 contiguous 5x5 m quadrats. All the advance growth was harvested for aging and the height, diameter and wet weight of the tallest individual in each plot were recorded. Each plot was subsampled by 5 1x1 m quadrats for litter, and after drying the weight of each sample was measured. At the centre of each plot the sky view factor was determined (for method see Chapter 2) and the distance to the nearest crown was recorded. The top 15 cm of mineral soil was collected from beneath the overwood and from the middle of the gap, to determine the pF curves of the soil samples following the procedure of Fawcett and Collis-George (1967).

Another six gaps were sampled by north-south and east-west 2

m wide belt transects to find the density and height of the tallest plants across the transition. The location and diameter of the trees surrounding the gap were noted.

In some heavily logged areas single trees may occur within dense patches of regeneration. At two such areas the diameter of six trees was measured and line transects were run out from the stem into regrowth of uniform size. The transects were orientated with the four cardinal points of the compass to record the diameter and density of the regrowth in 1 $m^2$ quadrats, and the width of the crown.

The relationship between height and sky view factor was found for 29 non-contiguous stems of varying sizes by felling the plant and then photographing the sky view with a hemispherical lens in the middle of the previous location at the crown.

An 80 m x 1 m belt transect was run through an area of unlogged forest and the height of all the advance growth and distance to the nearest stem and crown were recorded. In this area 149 trees were measured to find the stem diameter, tree height, height of the lowest branch, number of branches, and the width of the crown in order to provide data for a model to predict the amount of solar radiation on the forest floor in December and July (Nunez, 1984). The model was further employed to investigate the effect of gap creation on the forest floor radiation field. The amount of radiation across a 70 m north-south transect beneath the unlogged forest was estimated by the model. The change in the radiation was calculated after a gap

was created by the removal of two trees near the transect.

### 4.2.3 Results

Beneath the forest canopy the mean height of the tallest advance growth is highly correlated ($P<0.001$) to both the distance to the nearest crown edge and to the nearest stem. Regrowth density is also correlated with both of these measures of competition although less significantly ($P<0.02$). Neither height nor density correlated with the predicted estimates of sky view factor and summer or winter radiation.

The presence of mature trees has a marked effect upon the even-aged regeneration. Leaf shape, stem base diameter, and height all change across the competition gradient (Figures 4.1, 4.2 and 4.3). The highly intercorrelated measures of stem diameter, height, and wet weight all correlated with changes in overwood sky view factor and litter weight correlated with the height and diameter of the tallest stem across the gap (Figure 4.4). Soil texture, pH and total and available soil nutrients did not correlate with increased tree height. Similarly, the moisture-holding characteristics of the forest and gap soils were not found to be significantly different (Figure 4.5). However, the foliar concentrations of nitrogen ($P<0.01$) and sodium ($P<0.05$) are positively correlated with increased productivity.

Figures 4.3 and 4.6 show that the distribution of sapling height is symmetrical in the east-west plane but is asymetrical in the north-south plane where the tallest saplings occur in the

Figure 4.1. Change in leaf shape, stem base diameter and age across a regrowth gap.

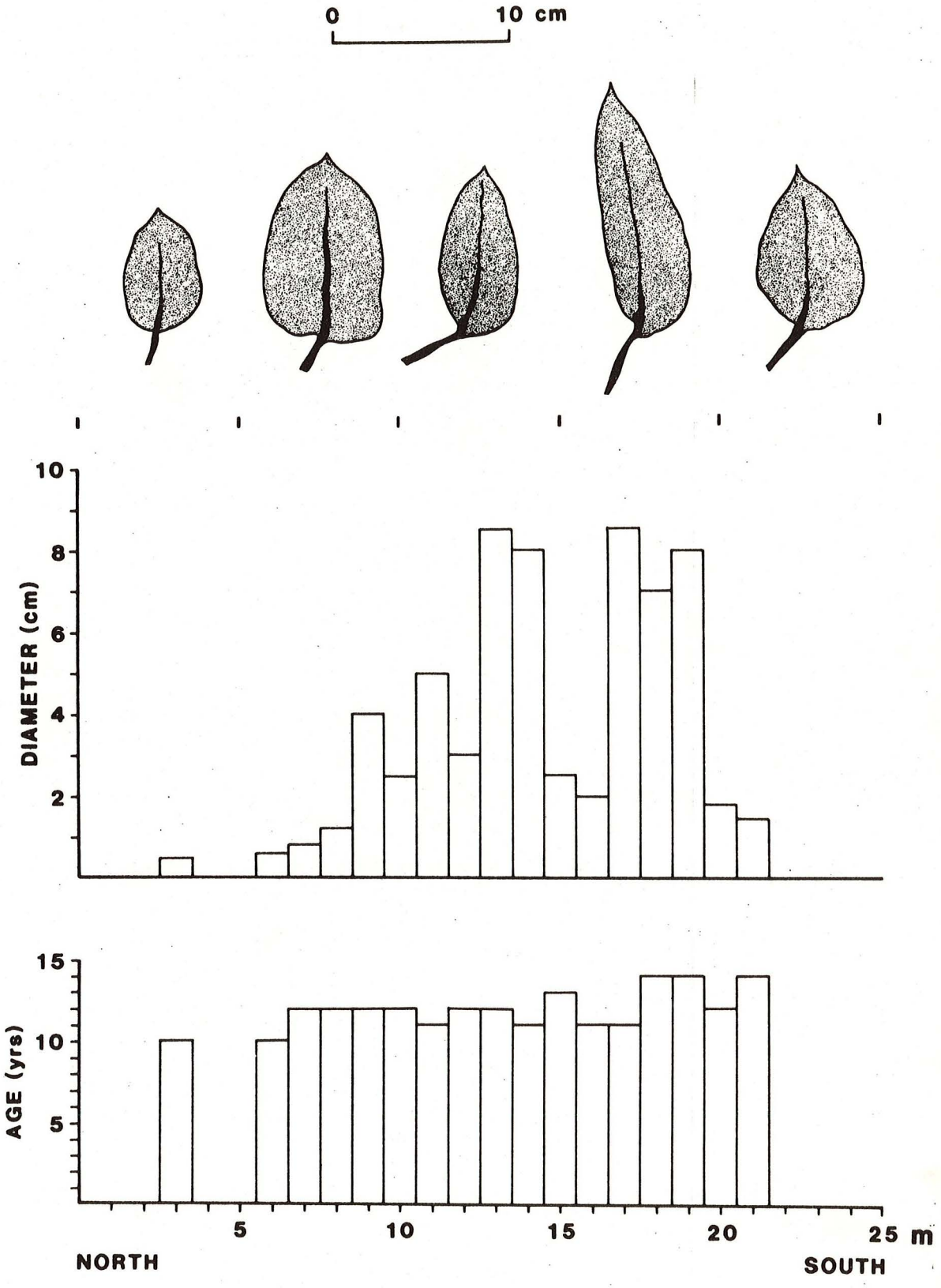

0
10 cm
DIAMETER (cm)
10
8
6
4
2
AGE (yrs)
15
10
5
5
10
15
20
25 m
NORTH
SOUTH

Figure 4.2. Effect of a single tree (dbhob=75 cm ) on the stem base diameter of the surrounding regrowth.

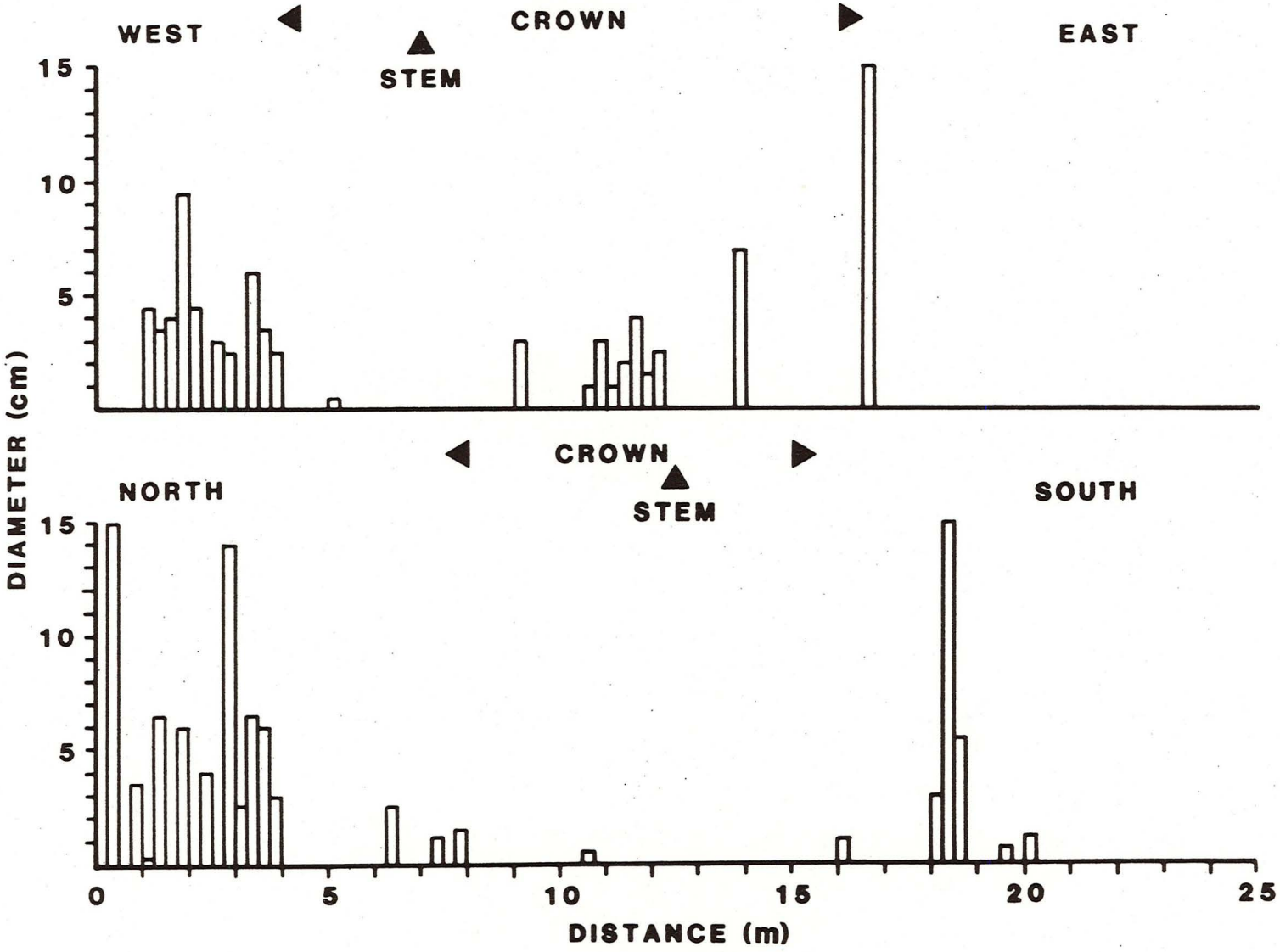
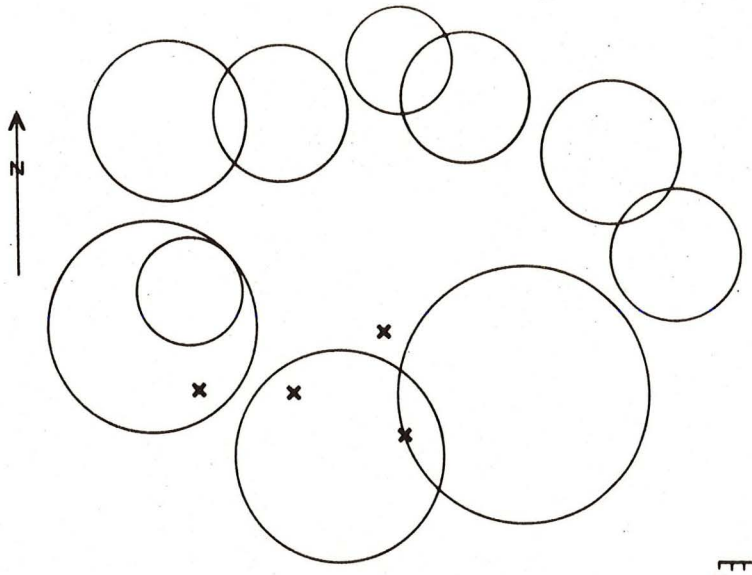
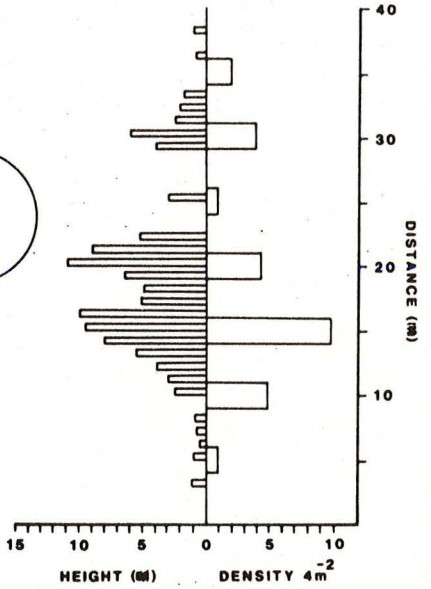

WEST
CROWN
EAST
STEM
15
10
5
DIAMETER (cm)
CROWN
NORTH
SOUTH
STEM
15
10
5
0
5
10
15
20
25
DISTANCE (m)

Figure 4.3. Change in height and density of regeneration across a forest gap. The crown diameter of surrounding trees is multiplied by the derived crown width/diameter ratio of 14.5 m (SE= 0.4, n=149). Crosses mark the position of stumps with a combined basal area of 5.69 $m^2$.


N


40
30
20
10
DISTANCE (m)
15
10
5
0
5
10
HEIGHT (m)
DENSITY 4m-2

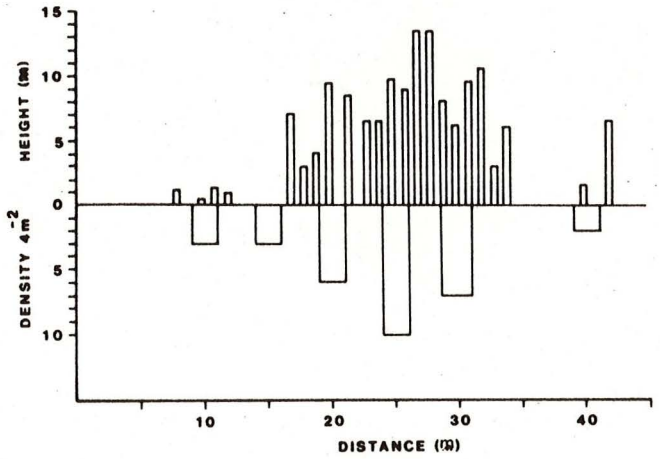

15
10
5
0
5
10
HEIGHT (m)
DENSITY 4m-2
10
20
30
40
DISTANCE (m)

Figure 4.4. Correlations between three measures of productivity and above ground environmental factors for twelve 25 $m^2$ plots across a gap.

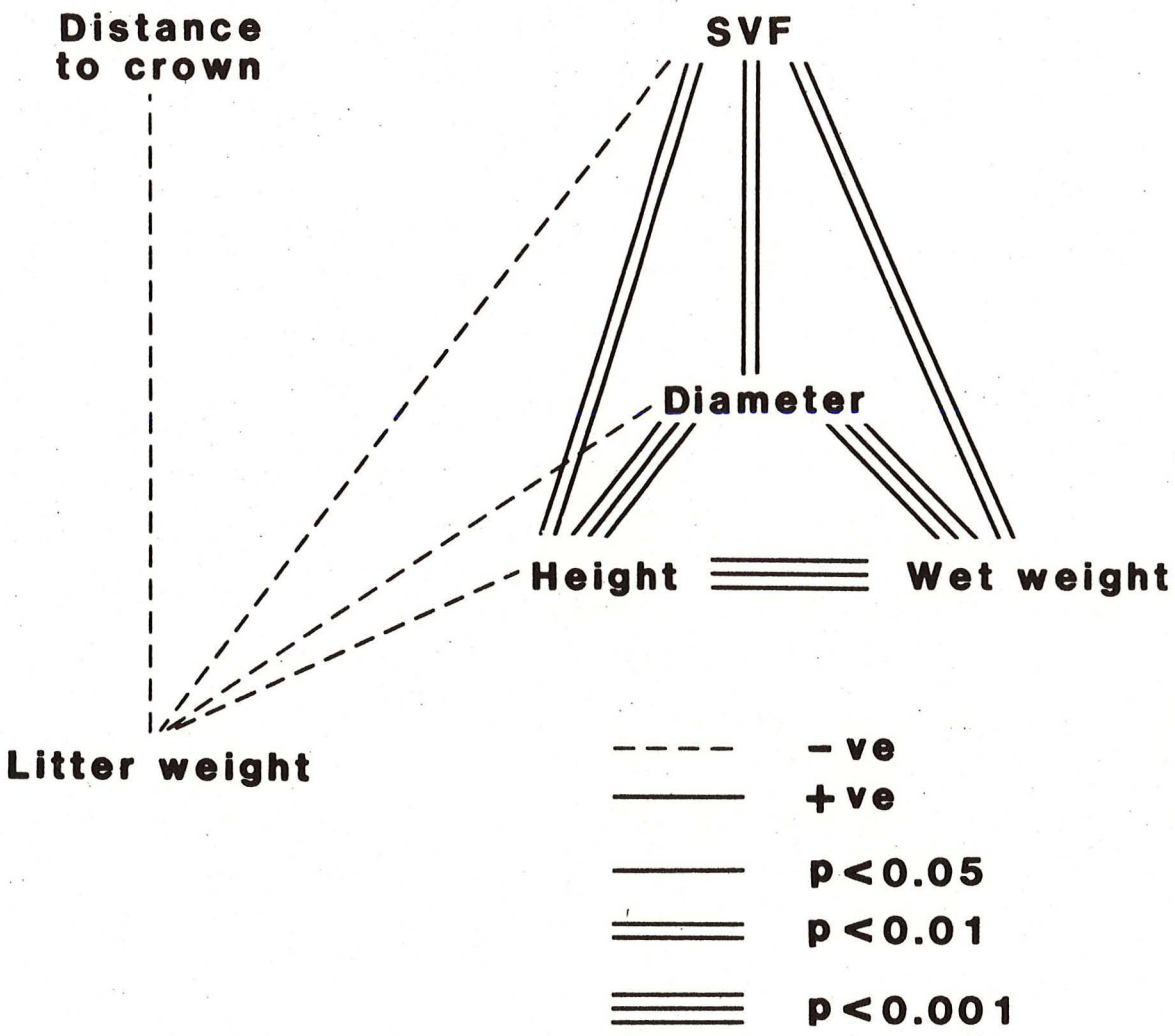

Distance to crown
SVF
Diameter
Height
Wet weight
Litter weight
- ve
+ ve
p<0.05
p<0.01
p<0.001

Figure 4.5. pF curves for the top 15 cm of forest and gap mineral soil. Comparison of the individual slopes for each soil type showed that they were not significantly different. The regression equation shown is derived from the combination of both data sets.

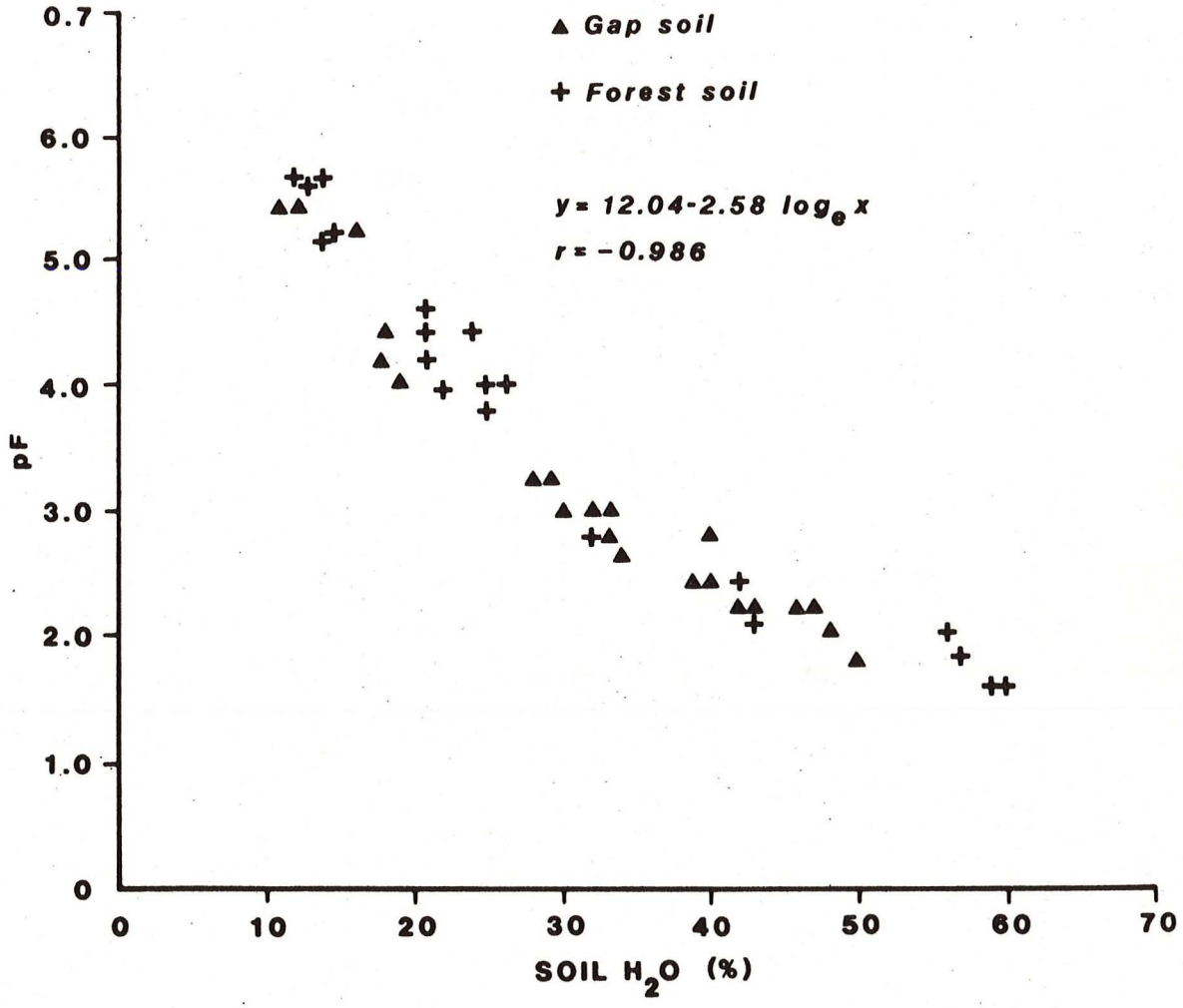

▲ Gap soil
+ Forest soil
y= 12.04-2.58 log_e x
r= -0.986
pF
0.7
6.0
5.0
4.0
3.0
2.0
1.0
0
0
10
20
30
40
50
60
70
SOIL H2O (%)

Figure 4.6. Mean east-west and north-south profile of 7 gaps. The tallest sapling is taken as the centre of each gap and the height of the surrounding regrowth is expressed as a percentage of the height of the central stem. Paired t-tests showed that both the 1-10 and 11-20 m sections of the east and west half and the 1-10 m north-south sides of the profile were not significantly different, but that the 11-20 ($P<0.05$) and 21-30 ($P<0.001$) m halves of the north-south profile were significantly different.

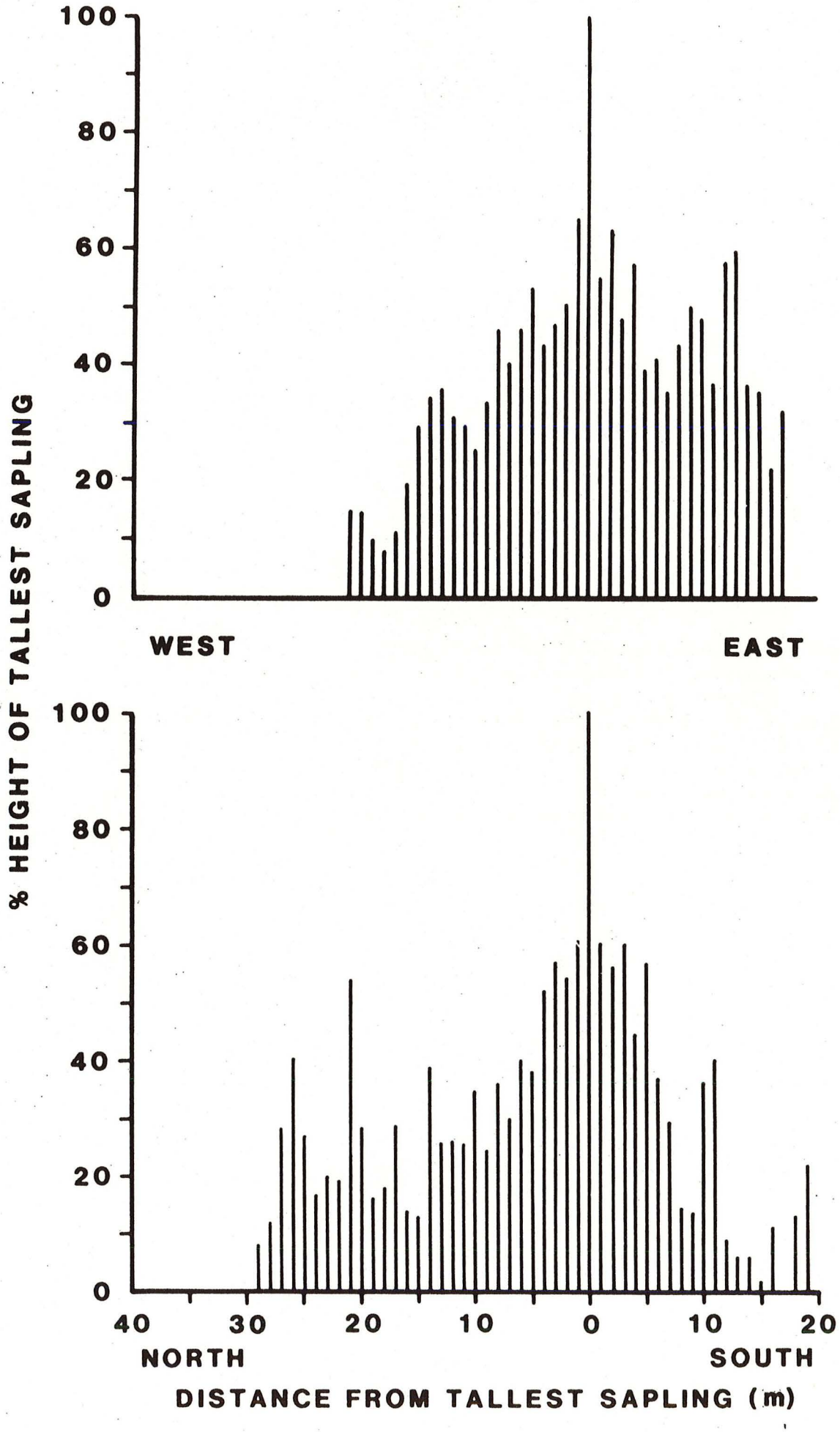
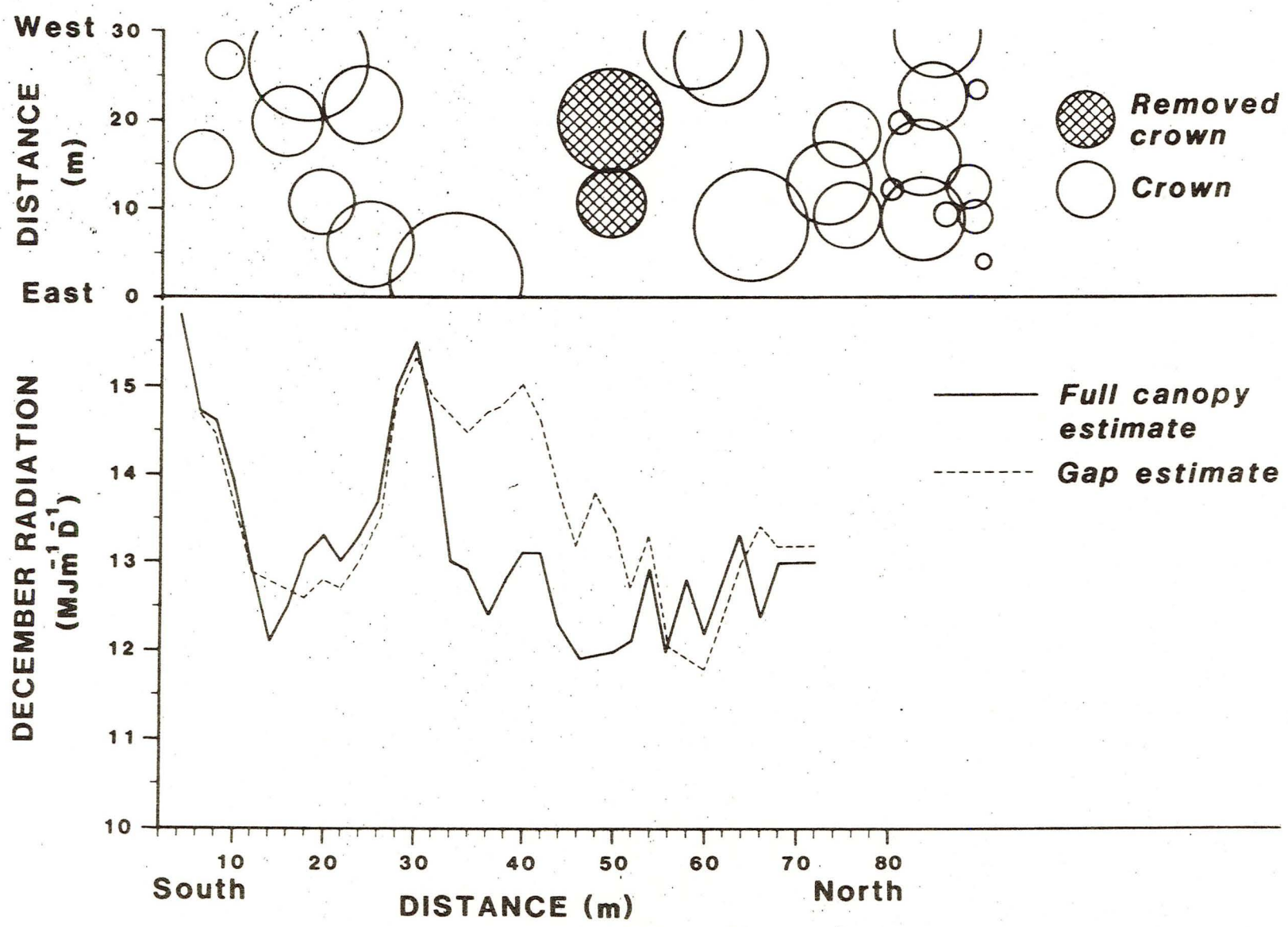

100
80
60
40
20
0
WEST
EAST
% HEIGHT OF TALLEST SAPLING
100
80
60
40
20
0
40
30
20
10
0
10
20
NORTH
SOUTH
DISTANCE FROM TALLEST SAPLING (m)

Figure 4.7. Predicted December radiation and sky view factor on the forest floor before and after the creation of a gap in which two trees were removed. The 70 m long and 1 m wide "transect" was run north-south from 15 m west of the eastern origin. (two trees removed) on a 35 m north-south transect.


West
East
DISTANCE (m)
30
20
10
0
Removed crown
Crown
DECEMBER RADIATION (MJm⁻¹D⁻¹)
15
14
13
12
11
10
Full canopy estimate
Gap estimate
10
20
30
40
50
60
70
80
South
North
DISTANCE (m)

southern part of the gap. Figure 4.7 shows that the polar quadrant of the gap receives the greatest amount of solar radiation. Furthermore, there is a non significant relationship ($P>0.05$) between height of gap regrowth and sky view factor (Figure 4.8). However,the significantly taller gap regeneration can have a lower S.V.F. than the stunted forest advance growth. Thus it appears that radiation is a secondary factor in controlling productivity, and only has a major influence on the dense stands of regrowth which occur in the absence of overwood competition (i.e. in gaps).

## 4.3 EXPERIMENTAL STUDIES OF COMPETITION BETWEEN TREES AND SEEDLINGS

### 4.3.1 Introduction

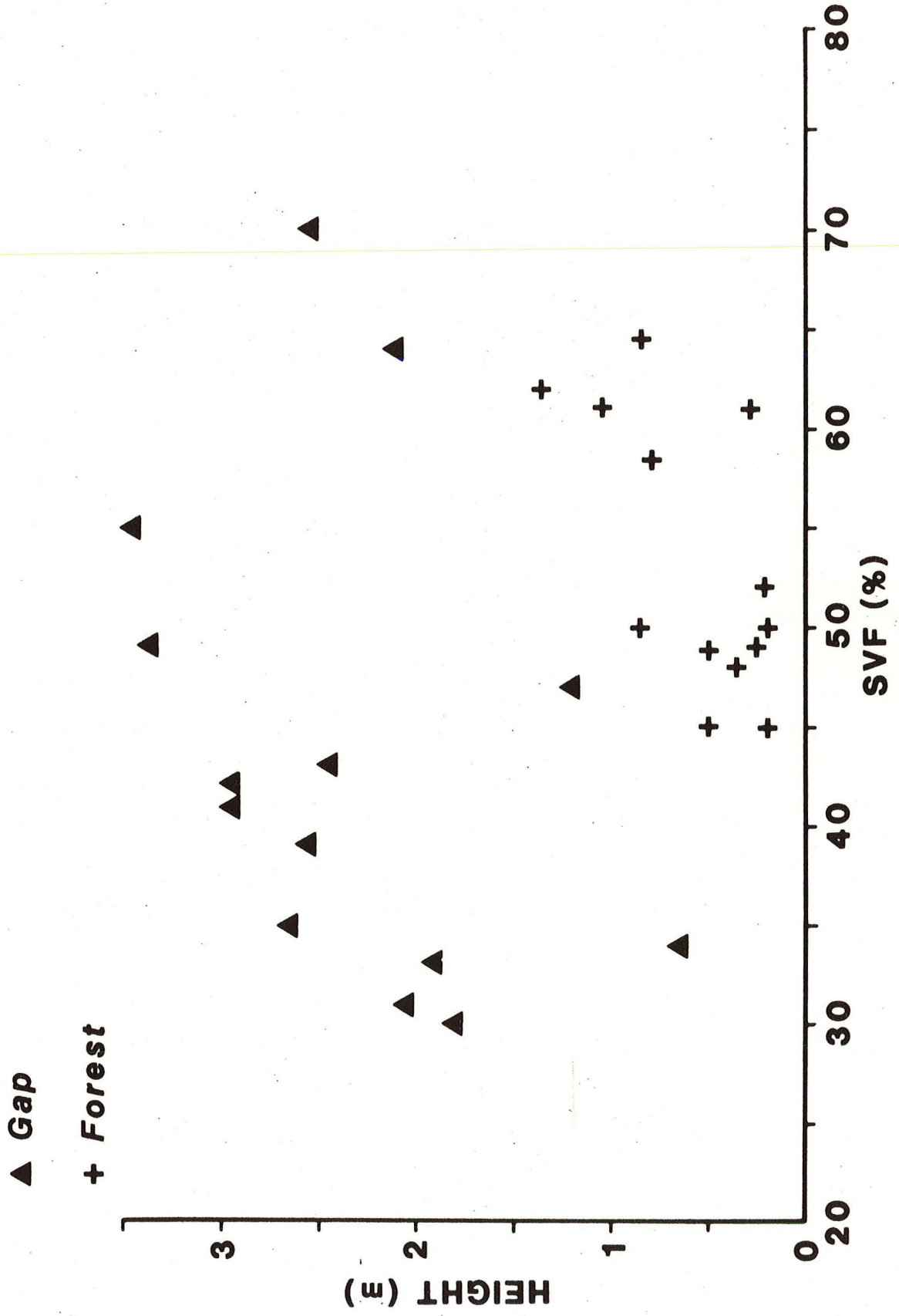
The studies of environmental correlates of the intraspecific competition gradient did not show that any factor was clearly limiting. The following experiments were designed to find what factors or interaction of factors cause suppressed growth of *E. delegatensis* regeneration.

### 4.3.2 Methods

#### 4.3.2.1 Studies of intraspecific allelopathy.

Twenty 1 g samples of *E. delegatensis* seed, that had been collected from the Great Lakes area by the Tasmanian Forestry Commission, were placed in petri dishes lined with moist filter paper and stratified for eight weeks. Following refrigeration the petri dishes were divided into four groups of five and the seeds

Figure 4.8. Relationship between height and the associated crown mid point sky view factor for forest and gap regeneration.


▲ Gap
+ Forest
HEIGHT (m)
0
1
2
3
20
30
40
50
60
70
80
SVF (%)

were grown under artificial illumination with a 12 hour photoperiod for two weeks. During the growing period three of the replicate blocks were irrigated with different extracts to test the hypothesis that substances in the roots, leaves or litter of E. delegatensis inhibit seedling growth when compared to growth of controls treated with distilled water. The extracts were prepared by filtering a 1:10 (w/w) fresh biomass-distilled water suspension after 24 hours of soaking at room temperature (procedure modified from del Moral et al., 1978). The number of ungerminated viable seeds as determined by the squash test (Boland et al. 1980a) and the length of the hypocotyl and radicle were recorded for each germinate after 14 days growth. A second bioassay was performed ,using similar procedures as above, on eight 1 g seed lots that were stratified for three weeks to test the inhibitory effect of leaf leachates from mature E. delegatensis leaves. The extract was prepared by washing 1140 grams of fresh mature leaves with 2.5 litres of distilled water. The washings were carried out by spraying a mist of water over the leaves which were laid out on a plastic sheet that drained into a collecting jar.

Seeds from 12 different trees were collected from the Waddamana area and following their stratification and germination were pricked out into 12 cm pots filled with sieved soil collected from the study site. At the two leaf stage the seedlings were divided into two groups of 175 plants. In each group 70 seedlings were randomly selected as controls, 70 were

treated with litter and 35 were treated with vermiculite and were arranged in a latin square design. The litter treatment consisted of covering the soil surface in each pot with about one cm of shredded, air dried forest litter and the second treatment consisted of a covering of vermiculite of similar depth. The plants were grown outside in Hobart with one block of 175 plants being frequently watered (watered treatment) and the other being less frequently watered (drought treatment) for a period of three months. At 6 and 12 weeks from the beginning of the experiment the height of the plants was measured from the soil to the growing tip.

4.3.2.2 Studies of above and below ground competition between mature trees and seedlings.

At five metre intervals across a 30 m north-south transect traversing a boundary from forest to a recently cleared area, soil samples were collected to ensure edaphic uniformity of pH, five total nutrients (N,P,K,Ca,Mg) , extractable phosphorus and soil texture (for methods see Chapter 2). At each five metre interval a plot was established where 15 seedings (mean height 11 cm) grown from seed collected from the locality and raised in a glasshouse by the CSIRO personnel, were planted out in a one $m^2$ area. Next to the control seedlings another 15 seedlings were planted in a one $m^2$ area that had been isolated from root competition. This isolation was achieved by creating a barrier to below ground competition by digging a 20-40 cm wide and c.50 cm deep circular trench through the root horizon in the rocky dolerite soil. A sturdy plastic sheet was wrapped around the one

m soil monolith and then buried by refilling the trench. All the seedlings were watered during drought conditions in the summer of 1981/82 and were protected from browsing by enclosure in wire cages. The height , number of leaves, leaf damage and root exposure were regularly recorded for a two year period from October 1981. The stomatal resistance of six plants in each plot was measured with a porometer at midday on the 20th of February, 1983.

To test the hypothesis that the inhibition of seedling growth beneath mature trees is due to competition for nutrients, two pairs of trenched-untrenched 1 m plots were established in the forest near the transect. In each treatment 30 seedlings (mean height 4.5 cm), grown from seed collected from the study area , were planted in two groups of 15. One group served as a control and the other group was fertilized with 10 g of Osmocote ©[1] slow release (8 to 9 month) fertilizer which was buried (c. 2 cm depth) at the base of each seedling. The seedlings were watered with equal quantities of water every week during the summer. The height growth of the 15 plants in each of the four treatments was recorded 15 weeks and then one year after establishment.

To test the effect of trenching on soil moisture availability three 1 $m^2$ trenched-untrenched paired plots were established at the beginning, middle and end of the transect. To eliminate the effect of ground cover transpiration the surface vegetation was scalped to form a bare soil surface. The top 15 cm

of mineral soil was sampled for 15 weeks over the summer of 1982/83 to find the difference in soil moisture content between the pairs of plots. The soil was collected with a specially designed stainless steel 4 cm diameter corer which was hammered into the ground to collect about 200 g (oven dry weight) of soil. At each plot, three samples were taken and stored in air tight 125 ml labelled glass jars. Soil water content was determined gravimetrically following oven drying at 105°C for at least 24 hours. Triplicate soil samples were also taken near each plot across the transect every week from 11/11/1982 until 20/2/1983 and monthly until 6/7/1983. Rainfall during this period was measured with a rain gauge positioned in the middle of the trenched-untrenched transect.

To help interpret the biological significance of the soil moisture study a glasshouse experiment was performed to find the relationship between soil water and plant water stress as measured by the xylem pressure potential. Eighty-two healthy plants (c. 20 cm in height) growing in sieved soil collected from the Waddamana study area were watered to field capacity (c. 45%) and placed in a glasshouse. Over a twenty day period the plants were kept unwatered and each day at between 6.00 and 7.00 am (day light saving time) the xylem pressure potential and the associated soil moisture was determined for a number of plants. The xylem pressure potential was measured with a sap pressure bomb by finding the sap balancing pressure for the whole plant. The soil moisture content of the soil in pots which contained the

decapitated or drought killed plants was determined for two soil samples from each pot following the previously described procedure . The moisture content of air dry soil was also determined by allowing 35 replicate 125 ml jars of forest soil to air dry at room temperature for 14 days.

4.3.3 Results

Extracts derived from air dry forest litter and fresh E. delegatensis tree roots did not significantly inhibit percentage germination or growth of either the hypocotyl or the radicle of germinates grown from stratified E. delegatensis seed. However the leaf extract did inhibit germination ($P<0.001$) and hypocotyl growth ($P<0.05$) when compared to the controls treated with distilled water. This effect may be due to the high osmotic concentration of the extract, because the less concentrated leaf leachate was found to have no significant effect on the development of stratified E. delegatensis seed when compared to the controls (Figure 4.9).

The results of the litter allelopathy pot experiment suggested that the above bioassay procedure may not be sensitive to detecting inhibitory substances in the litter. This may indicate that the vermicalite treatment was not comple was not completly biologically inert. For example, soil temperature or moisture status may have varied between the various treatments, hence accounting for the difference in seedling performance. The height growth of 12 week old E. delegatensis seedlings was found to be significantly ($P<0.001$) affected by both soil covering and

Figure 4.9. Mean and range of percentage germination, and mean and 95% confidence interval of hypocotyl and radicle growth of E. delegatensis germinates grown for two weeks and treated with either distilled water, root extract, litter extract, leaf extract or leaf leachate.

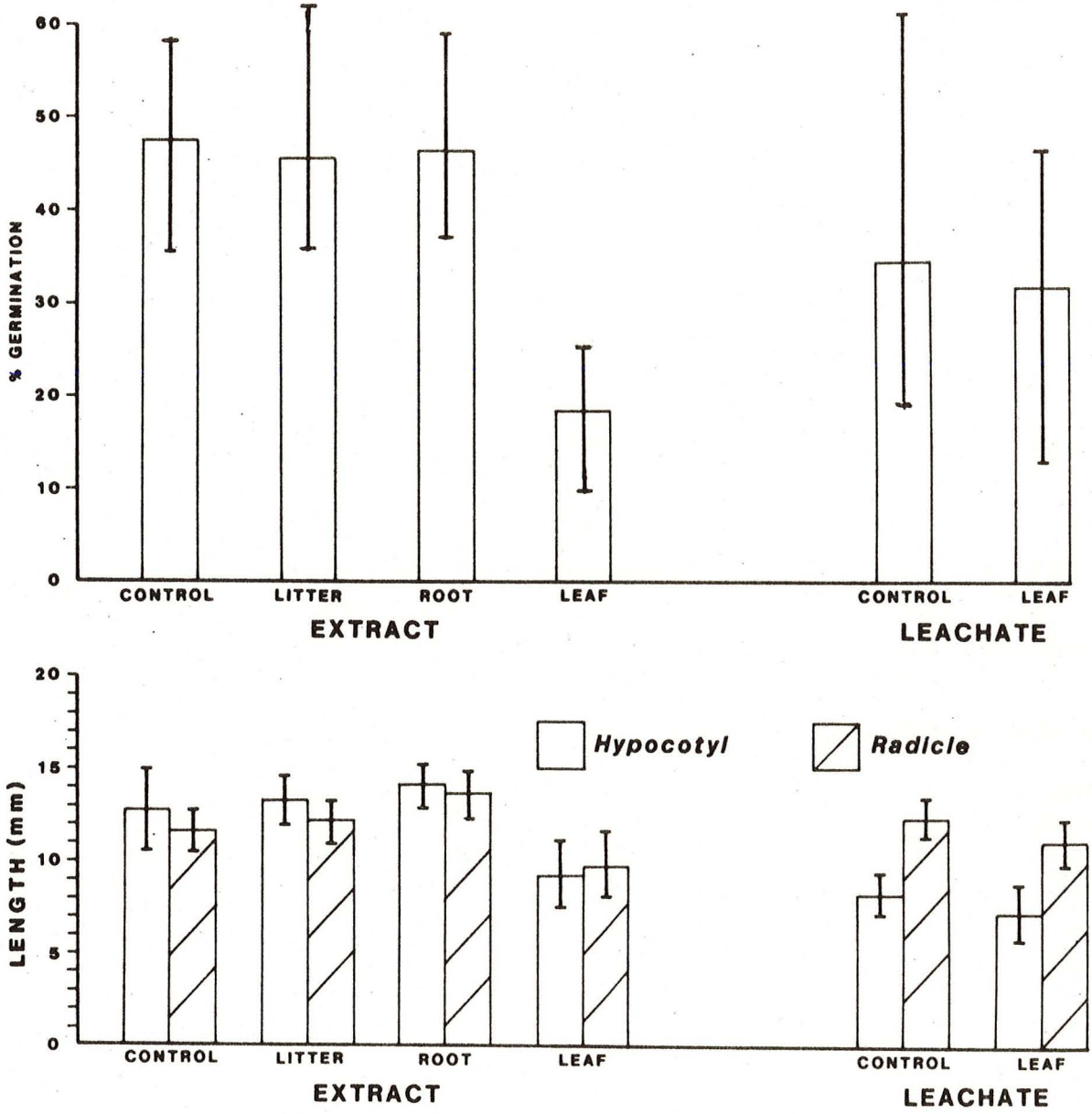
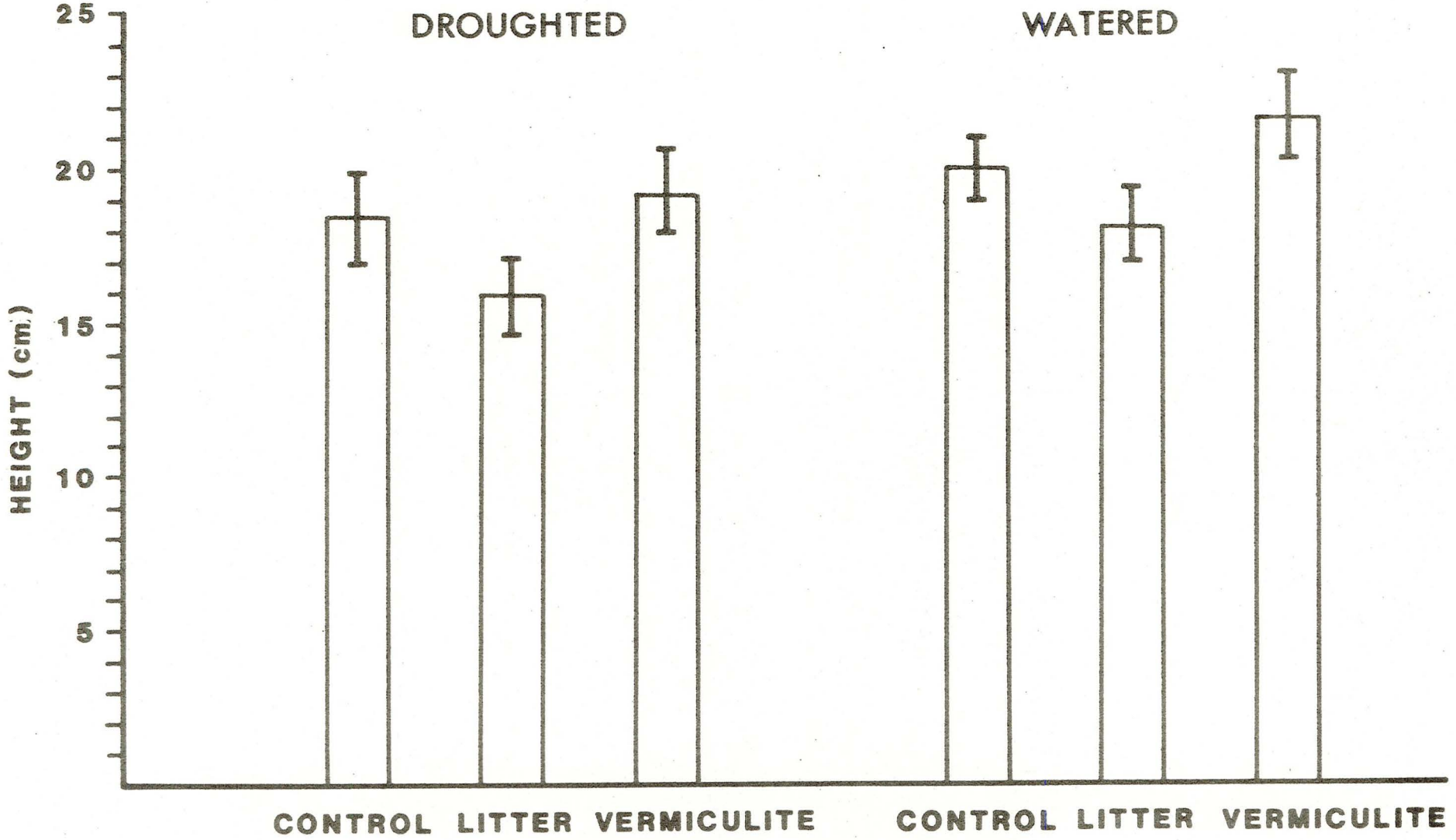

% GERMINATION
60
50
40
30
20
10
0
CONTROL
LITTER
ROOT
LEAF
CONTROL
LEAF
EXTRACT
LEACHATE
LENGTH (mm)
20
15
10
5
0
Hypocotyl
Radicle
CONTROL
LITTER
ROOT
LEAF
CONTROL
LEAF
EXTRACT
LEACHATE

Figure 4.10. Mean and 95% confidence interval height growth of E. delegatensis seedlings grown with no soil covering , litter soil covering and vermiculite soil covering for 12 weeks with two levels of watering , in the open at Hobart.


DROUGHTED
WATERED
HEIGHT (cm.)
25
20
15
10
5
CONTROL
LITTER
VERMICULITE
CONTROL
LITTER
VERMICULITE

watering regime, but analysis of variance revealed that there was not a significant interaction between these treatments (Figure 4.10). A least significant difference range test showed that for the pooled watered and droughted treatments a litter mulch caused significantly smaller height growth ($P<0.05$) when compared to the statistically similar height growth of the controls and seedlings treated with an inert mulch.

The growth of seedlings across the trenched-untrenched transect indicates that below ground competition is an important factor in causing seedling suppression. Two way analysis of variance of the heights of seedlings grown in the field for 23 months shows the highly significant ($P<0.001$) effect of both trenching and position on the competition gradient and a significant ($P<0.001$) interaction between these treatments. The height growth does not increase across the gradient from forest to the cleared area. This result is due, in part, to microclimatic effects associated with canopy removal and is discussed in the following chapter(see Plates 5.1 and 5.2). Figure 4.11 shows that three of the six plots across the gradient had significant ($P<0.05$) height differences between the trenched and untrenched treatments; the tallest plants occurring in the plots protected from root competition. This trend is supported by the results of the two fertilized-trenched combination studies where the unfertilized untrenched seedlings were significantly ($P<0.05$) smaller than the unfertilized trenched plants (Figure 4.12 and Plates 4.1 and 4.2). The results of this experiment indicate that the roots are not competing for nutrients. The

Figure 4.11. Mean and 95% confidence interval heights of trenched and untrenched seedlings planted along a transect traversing a forest edge and grown for 23 months at Waddamana.

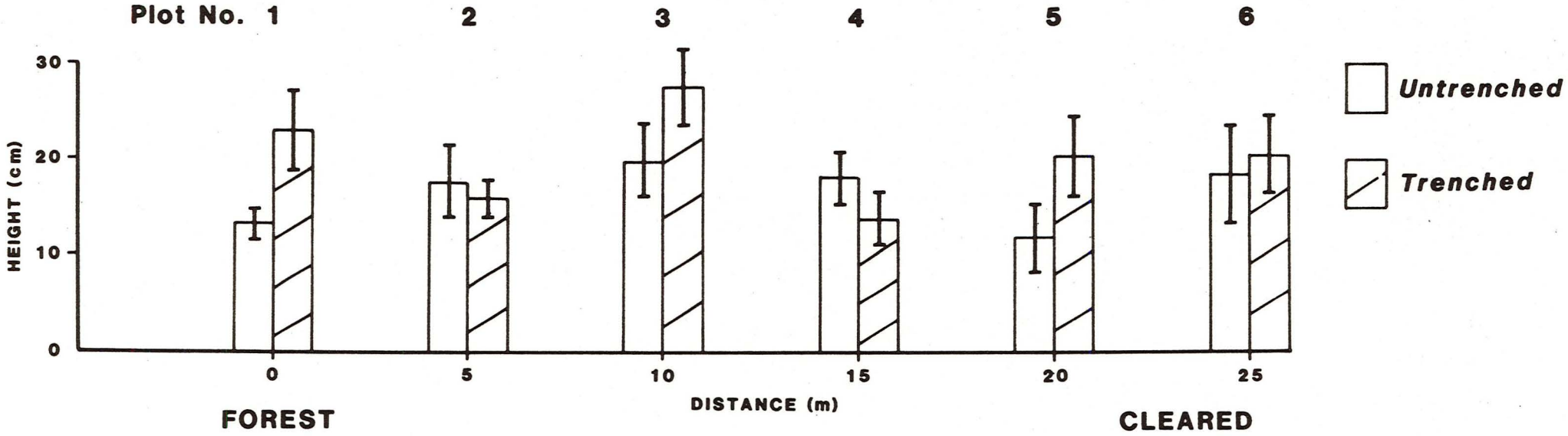

Plot No. 1
2
3
4
5
6
30
20
10
0
HEIGHT (cm)
0
5
10
15
20
25
DISTANCE (m)
FOREST
CLEARED
Untrenched
Trenched

Figure 4.12. Mean and 95% confidence interval for height growth of unfertilized untrenched , fertilized untrenched , unfertilized trenched , and fertilized trenched seedlings for two experimental plots beneath the forest canopy. Results for plot A refer to 15 weeks of growth, after which the seedlings were heavily browsed. Plot B was measured after one year of growth in the field.

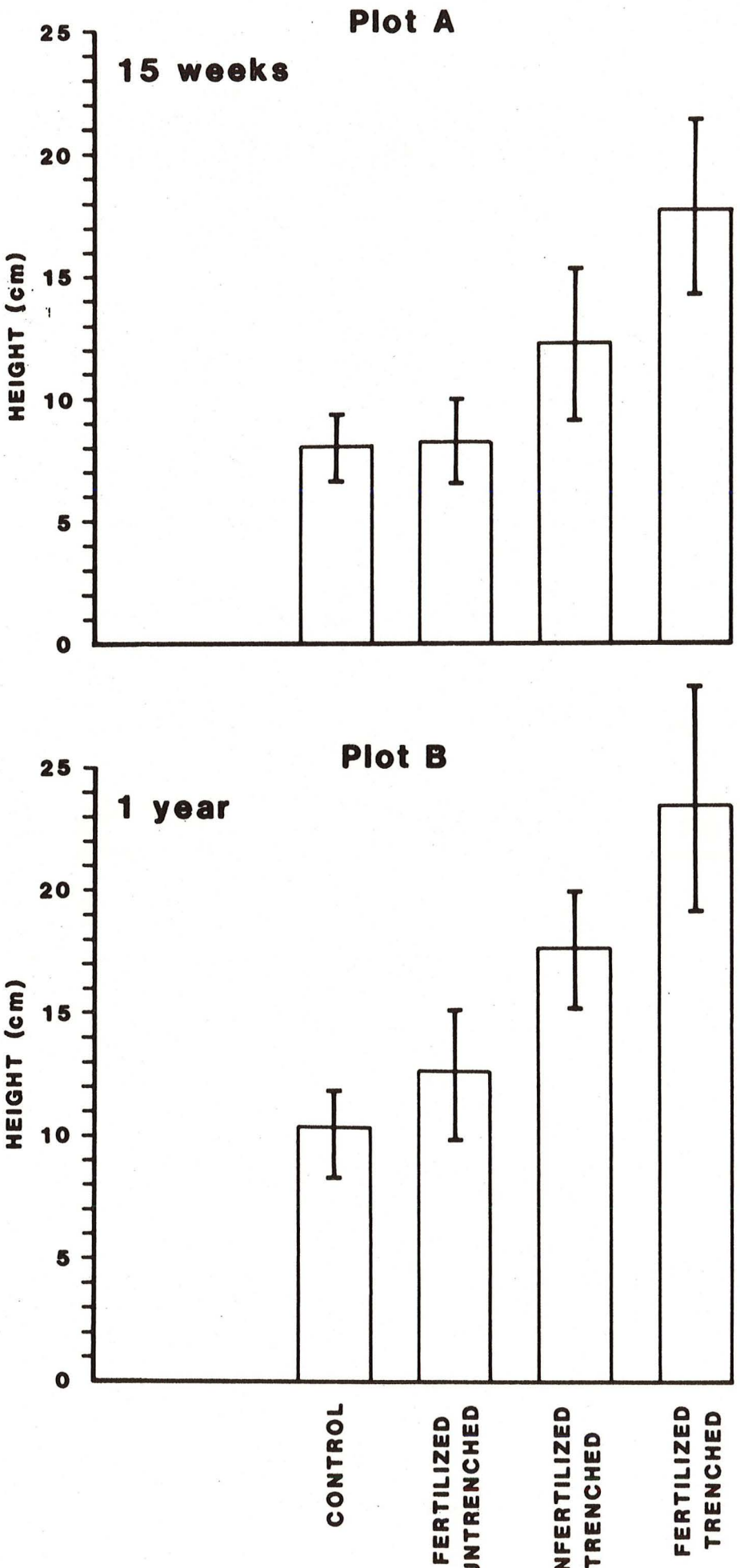

Plot A
15 weeks
HEIGHT (cm)
25
20
15
10
5
0
Plot B
1 year
HEIGHT (cm)
25
20
15
10
5
0
CONTROL
FERTILIZED UNTRENCHED
UNFERTILIZED TRENCHED
FERTILIZED TRENCHED

Plate 4.1. The fertilized trenched and untrenched seedlings grown in the forest.

Plate 4.2. The unfertilized trenched and untrenched seedlings grown in the forest.


Plot H
Inoculated No fert
15/2/03

untrenched fertilized seedlings are not significantly different from the controls and both are smaller ($P<0.05$) than the trenched unfertilized plants. Fertilization and trenching caused the most rapid growth of the seedlings.

Paired t-tests of the soil moisture content in trenched and untrenched plots with a barren soil surface showed that the trenched plots had significantly more moisture than the adjacent untrenched plots. Table 4.1 shows that the mean difference between the trenched-untrenched plots increases across the competition gradient from forest to the cleared area.

This trend is clearly evident for soil moisture content across the transect. Figure 4.13 shows the marked and statistically significant soil moisture differences between the soils beneath the forest (pooled from plots 1,2 and 3) and those out in the open (pooled from plots 4, 5 and 6). The differences become less significant after rainfall, but during the summer months this effect is short lived.

The glasshouse study of *E. delegatensis* seedling response to various levels of soil moisture indicates that when the content of soil water drops below 20% the plants become exponentially stressed until death at 13.4 % (SE 0.3%) soil moisture content (Figure 4.14). Figure 4.13 shows that the forest soil contained less than 20% moisture for 12 weeks during the summer of 1982/83 while the soil moisture content of the cleared area was only below this level for four weeks. Further, during the driest

TABLE 4.1

Mean difference and standard error of soil moisture content between paired trenched-untrenched plots across a transect from forest to a cleared area sampled for 15 weeks over the summer of 1982/82.

| | Forest<br>Plot 1 | Forest edge<br>Plot 3 | Cleared<br>Plot 6 |
|---|---|---|---|
| Mean difference | 3.1±0.8% | 3.3±1.2% | 8.4±1.3% |

Figure 4.13. Mean and 95% confidence interval of the soil moisture in the top 15 cm of soil at the forested and cleared ends of the trenched-untrenched transect from November 1982 to July 1983. The forest group is derived by pooling the mean values from the triplicate samples collected at plots 1,2 and 3. The cleared soil group is similarly derived from plots 4,5 and 6. The amount of rain that fell between soil samplings is also shown.

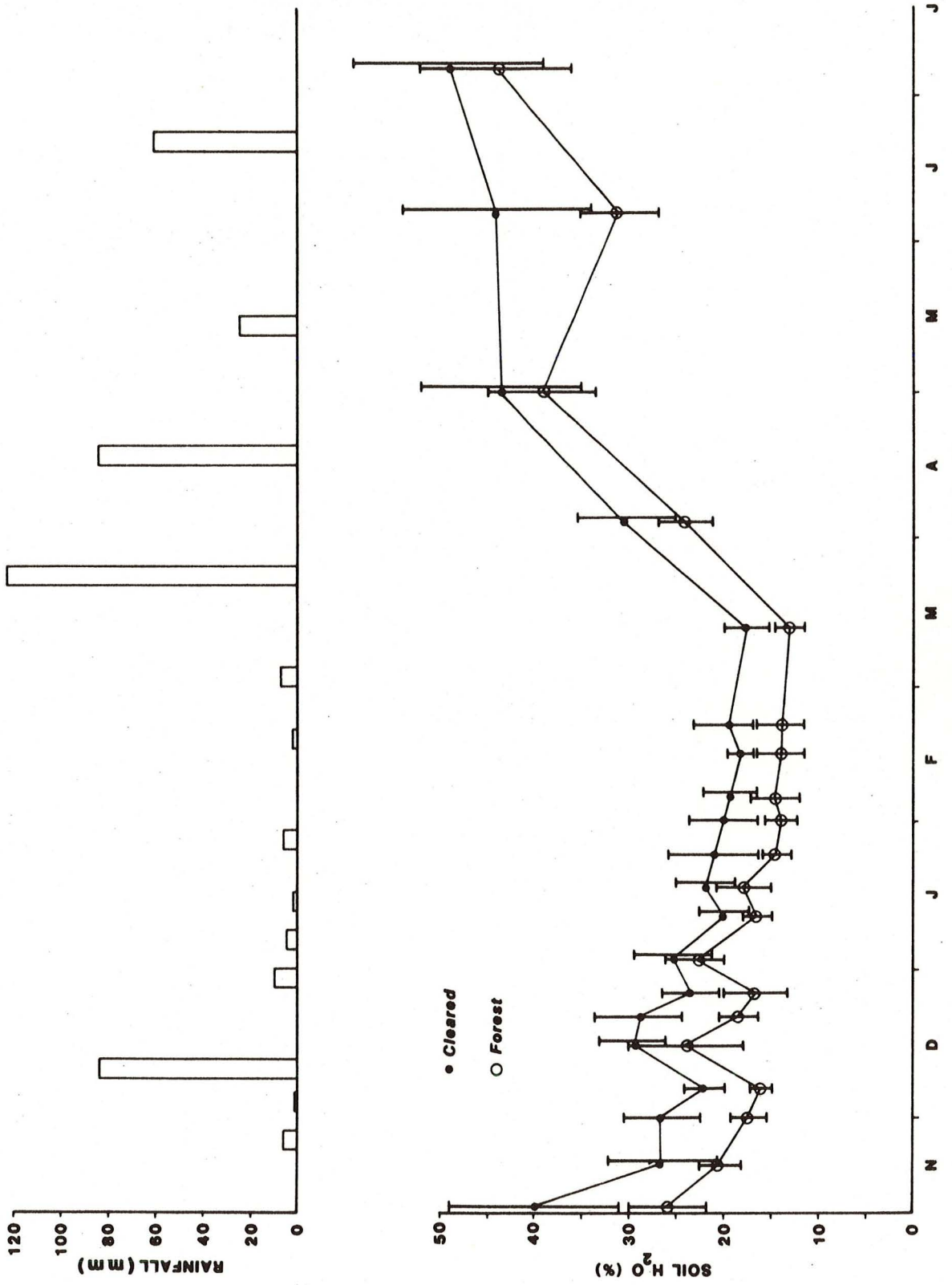
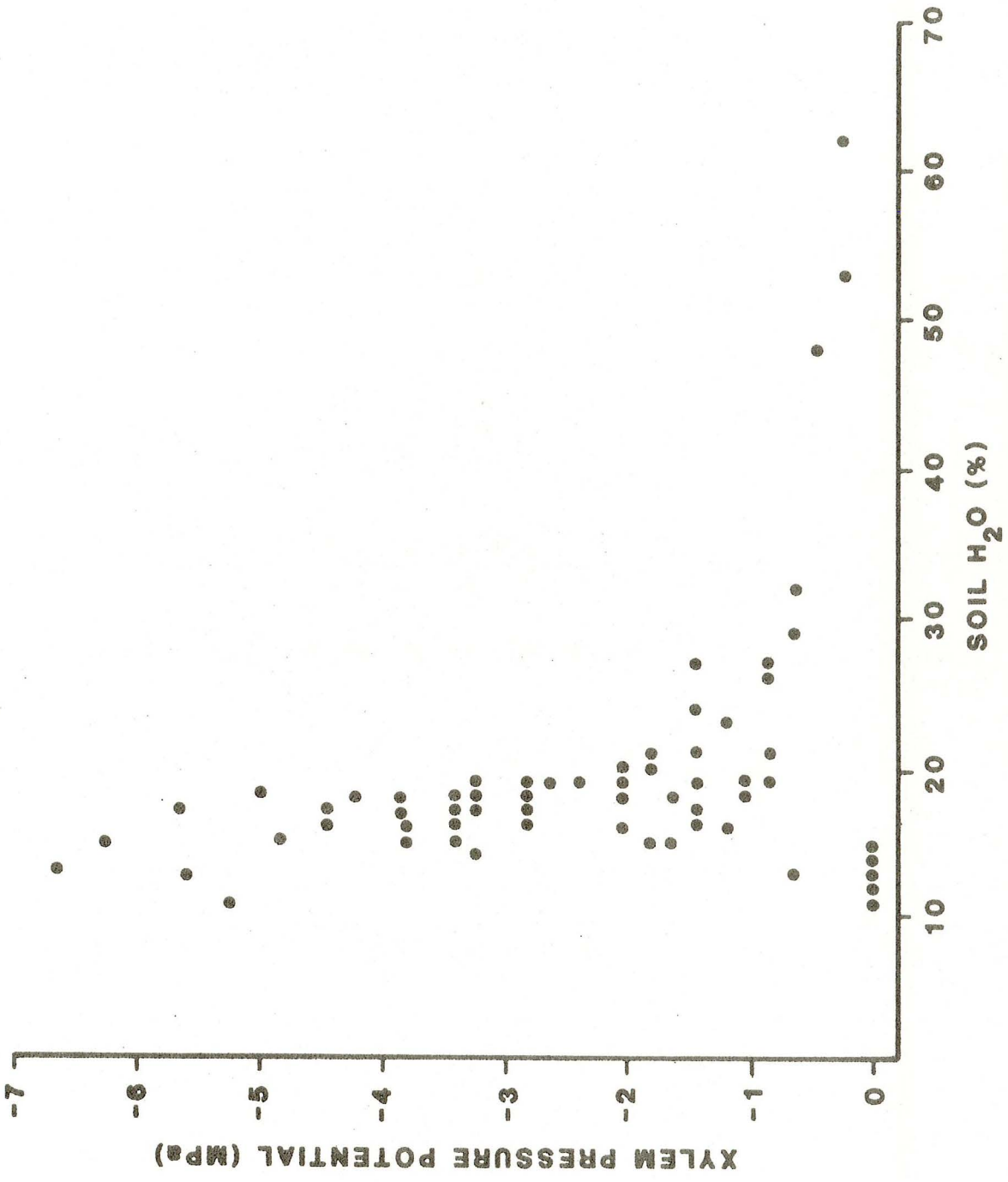

RAINFALL (mm)
120
100
80
60
40
20
0
SOIL H2O (%)
50
40
30
20
10
0
• Cleared
○ Forest
N
D
J
F
M
A
M
J
J

Figure 4.14. Relationship between xylem pressure potential and soil moisture content. The soil was found to be air dry at 8.2 (SE=0.2%), and plant death occured at 13.4(SE=0.3%) soil moisture.


XYLEM PRESSURE POTENTIAL (MPa)
-7
-6
-5
-4
-3
-2
-1
0
10
20
30
40
50
60
70
SOIL $H_2O$ (%)

month, February, the forest soils had less than 15% water in the top 15cm. The survival of the unwatered one year old seedlings across the transect during this period of drought probably reflects the fact that the plants had established roots at depth in the soil profile.

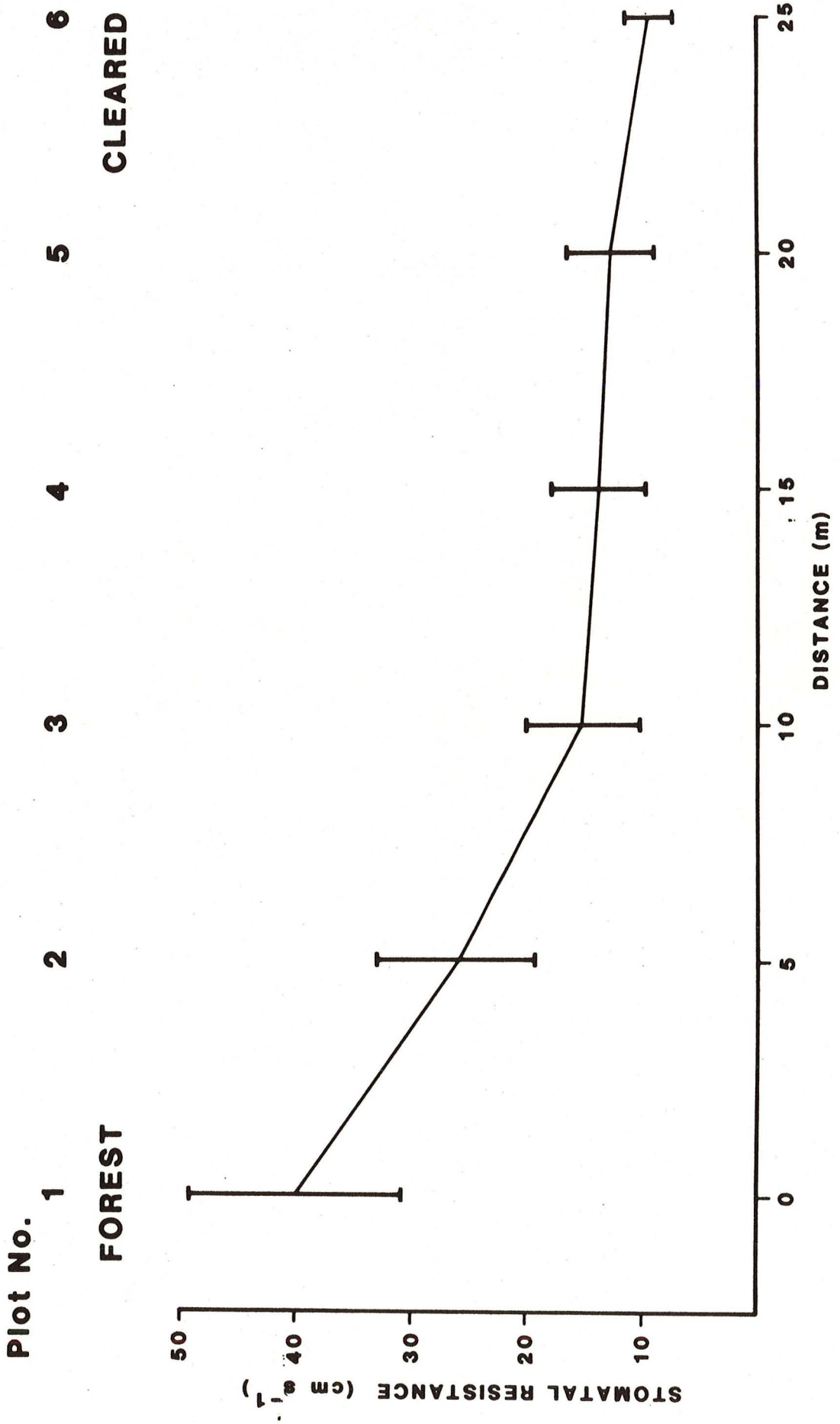
Analysis of variance of the logarithm transformed stomatal resistance values determined for six plants in each plot across the transect during February, showed that at this stage in the drought, the trenching treatment had no significant effect upon the level of drought stress in the seedlings. However, the analysis showed there was a marked position effect ($P<0.001$). Figure 4.15 shows that the level of water stress steadily declines across the transect. At the time of sampling there was a marked top soil moisture gradient ranging from the lowest value of 13% beneath the canopy to the maximum of 20% in the cleared area.

## 4.4 EXPERIMENTAL STUDIES OF SUPPRESSION AND RELEASE OF E. DELEGATENSIS ADVANCE GROWTH.

### 4.4.1 Introduction

The results of the above experiments indicate that seedling suppression may be related to an allelopathic influence from the forest litter as well as to competition with the overwood for water. The following experiments were designed to determine the environmental conditions necessary for the release of the advance growth.

Figure 4.15. Mean and 95% confidence interval of the stomatal resistance derived from pooled trenched and untrenched seedlings across the competition gradient.


Plot No.
1
2
3
4
5
6
FOREST
CLEARED
STOMATAL RESISTANCE (cm s⁻¹)
50
40
30
20
10
0
5
10
15
20
25
DISTANCE (m)

4.3.2 Methods

Twelve groups of twenty suppressed advance growth saplings, ranging in height from 0.5-1.5 m, were randomly selected and tagged in the small area (c.0.5 ha) of unlogged forest at the Waddamana experimental site. Each group of the randomly distributed individuals was measured to find the height of the stem from the ground to the growing tip(stems were straightened for measurement) and the number of green healthy leaves. A combination of treatments was applied to measure the effect of fertilization, litter cover, inert mulching, and understorey competition on the growth rate of the saplings. The fertilized plants received 0.5 kg of E.Z. Lightning Mix NPK fertilizer spread evenly to form a semi-circle ( radius =0.5 m) around the stem. Competition was removed by scalping the ground cover within a 0.5 m radius of the treated plant. Similarly, the effect of forest litter was removed by raking away any dead plant material surrounding the advance growth. The inert mulch treatment consisted of a one $m^2$ sheet of heavy hessian that was positioned on the ground so that the stem was in the centre of the sacking. The above treatments were combined to test their interaction. However, the experiment was not factorial because it was impossible to combine the inert mulch treatment with the effect of understorey competition. Ten plants, comparable to the controls in the first experiment and growing in a variety of positions in the forest, were measured and treated by surrounding the root system with plastic sheet in a circular trench, one metre in diameter and half a metre deep, in order to eliminate

below ground competition with the overstorey. All the above 250 plants were remeasured 12, 15, and 25 months following the establishment of the experiment in November 1981.

The effect of overstorey removal on suppressed saplings was determined by monitoring the growth of the plants following 100% and 50% canopy removal in two small areas of forest adjacent to the unlogged forest discussed above. Sixty plants in the shelterwood area and 40 saplings growing on the cleared area were measured to find their height and leaf number in April 1982 and were remeasured 8, 12 and 20 months later.

On four days during the driest month of the 1982/83 summer the level of drought stress experienced by the saplings growing on the cleared area and beneath the forest was indicated with the aid of a sap-pressure bomb. The xylem pressure potential of five leaves picked from five randomly selected plants on each site was determined regularly (c. hourly) from the early morning until dusk. At 8.00 am on the 19/2/1983 the water stress of six plants treated with trenching, and six that were irrigated with 60 litres of water each week for ten weeks, were compared to the stress measured in plants growing beneath the canopy and in the cleared area. At midday on the 19/2/83 the stomatal resistance of one leaf on each of ten plants growing on each canopy treatment was measured.

### 4.4.3 Data Analysis

To remove the effect of initial plant size from the growth response to the various experimental treatments an index of relative growth rate was calculated (Radford,1967). Relative growth rate (RGR) was defined as:

$$RGR = \frac{(\log_e Bt0 - \log_e Bt1)}{t} \times 100$$

where

Bt1 = initial biomass
Bt0 = final biomass
t = time in months

To test that RGR was independent from initial plant size, the significance of the correlation between initial biomass (height or leaf number) and the relative growth rate of either height or leaf number was determined. The mean relative growth rate of both height and leaf number for each treatment was converted into the mean annual percentage growth increment by employing the formula:

$$\%\text{Growth increment} = \left( e^{\left(\frac{RGRxt}{100}\right)} - 1 \right) \times 100$$

Analysis of variance was carried out on both the leaf and height RGRs to test the effect of and interaction between fertilizer - litter cover - understorey competition and

fertilizer - litter cover - hessian mulch. Treatments which were found to have no direct or interactive effect ($P<0.05$) on height or leaf growth were pooled with either the control or fertilized blocks for further analysis.

One way analysis of variance was conducted to test whether the 50% and 100% canopy removal treatments had a significant effect on the growth response when compared to either the control, fertilized or trenched treatments beneath the full canopy. The level of difference between the means of the above treatments was determined by employing two tailed t-tests.

4.4.4 Results

The index of relative growth rate for leaf number and stem height was found to be non-significantly correlated with initial plant size for all treatments apart from one case in which initial leaf number correlated to the RGR of leaves at the 0.05 level of significance (Table 4.2). The relative growth rate of height was less sensitive to the various treatments than was the change in leaf number.

Fertilization and the interaction between fertilization and litter cover were found to have a significant effect upon height growth ($P<0.01$, Table 4.3). The plants grown with fertilizer but in the absence of litter grew more than those treated with both litter and fertilizer. This trend was reversed in the case of the unfertilized stems (Table 4.2). A three way interaction between fertilizer - litter cover-hessian mulch was significant at the

# TABLE 4.2

Significance of correlations between initial size and the associated relative growth rate, mean and standard error of relative growth rates, and percentage mean annual increment of stem height and leaf number for all experimental treatments. Statistics are also shown for combined treatments which were shown to be not significantly different by analysis of variance ( Table 4.3).

| Treatment | | Stem height growth | | | | Number of leaves produced | | | |
|---|---|---|---|---|---|---|---|---|---|
| Key: Fer = Fertilizer, LC = Litter cover, HM = Hessian mulch, UC = Understorey competition, + = presence, - = absence | n | Significance of correlation. Initial height with RGR(M) | Mean relative growth rate | Standard error | % Annual Increment | Significance of correlation. Initial leaf No. with RGR(L) | Mean relative growth rate | Standard error | % Annual leaf production |
| Forest + Fer + LC + HM - UC | 20 | N.S. | 0.6095 | 0.1671 | 7.6 | N.S. | 1.3022 | 0.3921 | 16.9 |
| + Fer + LC - HM + UC | 20 | N.S. | 0.7846 | 0.1213 | 9.9 | N.S. | 2.1105 | 0.5023 | 28.8 |
| + Fer + LC - HM - UC | 20 | N.S. | 0.4899 | 0.1131 | 6.1 | N.S. | 1.2818 | 0.3425 | 16.6 |
| + Fer - LC + HM - UC | 20 | N.S. | 0.3672 | 0.1168 | 4.5 | N.S. | 1.3906 | 0.3559 | 18.2 |
| + Fer - LC - HM + UC | 20 | N.S. | 1.0193 | 0.1382 | 13.0 | N.S. | 3.0058 | 0.4175 | 43.4 |
| + Fer - LC - HM - UC | 20 | N.S. | 0.8023 | 0.1441 | 10.1 | N.S. | 2.1619 | 0.4696 | 29.6 |
| - Fer + LC + HM - UC | 20 | N.S. | 0.5217 | 0.1039 | 6.5 | N.S. | 1.3089 | 0.2894 | 17.0 |
| - Fer + LC - HM + UC | 20 | N.S. | 0.6010 | 0.1405 | 7.4 | N.S. | 0.1467 | 0.4223 | 1.7 |
| - Fer + LC - HM - UC | 20 | N.S. | 0.5066 | 0.1130 | 6.3 | N.S. | 0.7895 | 0.4647 | 9.9 |
| - Fer - LC + HM - UC | 20 | N.S. | 0.6358 | 0.0937 | 7.9 | $P < 0.05$ | 0.5589 | 0.3393 | 6.9 |
| - Fer - LC - HM + UC | 20 | N.S. | 0.3377 | 0.0806 | 4.1 | N.S. | -0.0175 | 0.3601 | -2.1 |
| - Fer - LC - HM - UC | 20 | N.S. | 0.3616 | 0.1607 | 4.4 | N.S. | 0.9778 | 0.3587 | 4.4 |
| trenched | 10 | N.S. | 0.2312 | 0.5482 | 2.8 | N.S. | 3.3960 | 0.6528 | 50.3 |
| Pooled - Fer + LC ± UC | 40 | - | 0.5538 | 0.0893 | 6.9 | - | - | - | - |
| Pooled + Fer + LC ± UC | 40 | - | 0.6372 | 0.0852 | 7.9 | - | - | - | - |
| Pooled - Fer + UC ± LC | 40 | - | - | - | - | - | 0.0646 | 0.2740 | 0.8 |
| Pooled + Fer + UC ± LC | 40 | - | - | - | - | - | 2.5581 | 0.3300 | 35.9 |
| Shelterwood | 60 | N.S. | 0.3029 | 0.0587 | 3.7 | N.S. | 2.6571 | 0.3118 | 37.6 |
| Clearfell | 40 | N.S. | 0.4520 | 0.0860 | 5.6 | N.S. | 2.9385 | 0.5315 | 42.3 |

TABLE 4.3

Significance of main effects and interactions of various treatments upon leaf number and stem height growth rates for A) fertilizer-litter cover-understorey competition, and B) fertilizer-litter-cover hessian mulch experiments.

| | Treatment | Relative growth rate: leaf number | Relative growth rate: stem height |
|---|---|---|---|
| A. | Fertilizer | $P < 0.001$ | $P < 0.01$ |
| | Litter cover | N.S. | N.S. |
| | Understorey competition | N.S. | N.S. |
| | Fertilizer x litter cover | N.S. | $P < 0.01$ |
| | Fertilizer x understorey competition | $P < 0.01$ | N.S. |
| | Litter cover x understorey competition | N.S. | N.S. |
| | Fertilizer x litter cover x understorey competition | N.S. | N.S. |
| B. | Fertilizer | $P < 0.05$ | N.S. |
| | Litter cover | N.S. | N.S. |
| | Hessian mulch | N.S. | N.S. |
| | Fertilizer x litter cover | N.S. | N.S. |
| | Fertilizer x hessian mulch | N.S. | N.S. |
| | Litter cover x hessian mulch | N.S. | N.S. |
| | Fertilizer x litter cover x hessian mulch | N.S. | $P < 0.05$ |

0.05 level (Table 4.2). However there was no apparent biologically meaningful cause of this significant interaction. The height growth of the sixty shelterwood plants was found to be significantly less than that of the controls ($P<0.05$) and the fertilized stems ($P<0.01$) grown beneath the full canopy (Table 4.4). There was no significant difference ($P>0.05$) detected between the height growth of the 100% canopy removal, and trenched treatments when compared to the controls.

Fertilization was found to have a significant effect ($P<0.05$) on the production of leaves in the fertilizer - litter cover - understorey competition experiment (Table 4.3). Similarly, fertilizer significantly ($P<0.001$) increased leaf production in the fertilized - litter cover - understorey competition experiment. However, in this experiment, there was a significant interaction ($P<0.01$) between fertilizer and understorey competition in that the addition of fertilizer and the presence of understorey competition resulted in greater growth compared to the fertilized stems growing in the absence of competition. In the case of the unfertilized plants the removal of understorey vegetation resulted in greater productivity when compared to the advance growth which competed with the understorey (Tables 4.2 and 4.3).

Leaf production of the forest controls proved to be significantly lower ($P<0.001$) than the fertilized, trenched, shelterwood and clearfell treatments. Table 4.4 shows that none of the latter treatments produced growth responses that

TABLE 4.4

t-test comparison of mean relative growth rates of stem height and leaf number for five different treatments and the calculated percentage mean annual increment.

Stem Height

| Treatment | $\bar{x}$ annual increment (%) | Control 6.9 | Fertilized 7.9 | Trenched 2.8 | Shelter-wood 3.7 | Clear-felled 5.6 |
|---|---|---|---|---|---|---|
| Control | 6.9 | - | | | | |
| Fertilized | 7.9 | NS | - | | | |
| Trenched | 2.8 | NS | NS | - | | |
| Shelterwood | 3.7 | P<0.05 | P<0.01 | NS | - | |
| Clearfelled | 5.6 | NS | NS | NS | NS | - |

Leaf Number

| Treatment | $\bar{x}$ annual increment (%) | Control 0.8 | Fertilized 35.9 | Trenched 50.3 | Shelter-wood 37.6 | Clear-felled 42.3 |
|---|---|---|---|---|---|---|
| Control | 0.8 | - | | | | |
| Fertilized | 35.9 | P<0.001 | - | | | |
| Trenched | 50.3 | P<0.001 | NS | - | | |
| Shelterwood | 37.6 | P<0.001 | NS | NS | - | |
| Clearfelled | 42.3 | P<0.001 | NS | NS | NS | - |

significantly differed from each other.

The trenched and control plants were found to have similarly high levels of water stress on the morning of 19/2/1983 as opposed to similarly low levels of stress recorded for the plants treated by watering and those treated by 100% canopy removal (Table 4.5).

The significant difference between the forest and clearfell treatments was constant throughout four days of sampling during the driest month in the summer of 1982/83 (Figure 4.16 ). The plants on the clearfelled site showed greater diurnal variation than the plants competing with the overstorey. In the mornings the plants on the clearfelled site had xylem water potentials greater than -1.0 MPa, while the stems in the forest had values less than -1.5 MPa. In the middle of the day there was statistical convergence in the measured water stress of plants in both treatments. However, at all sampling times the clearfell treatment had mean xylem water potentials that were greater than the means recorded from the plants growing in the forest.

The effect of overwood competition on the water relations of the advance growth is also apparent in Table 4.6, where increased levels of overwood cause the advance growth to increase its stomatal resistance.

TABLE 4.5

Mean and standard error xylem pressure potentials of advance growth in four experimental treatments at 8.00 a.m., 19.2.1983.

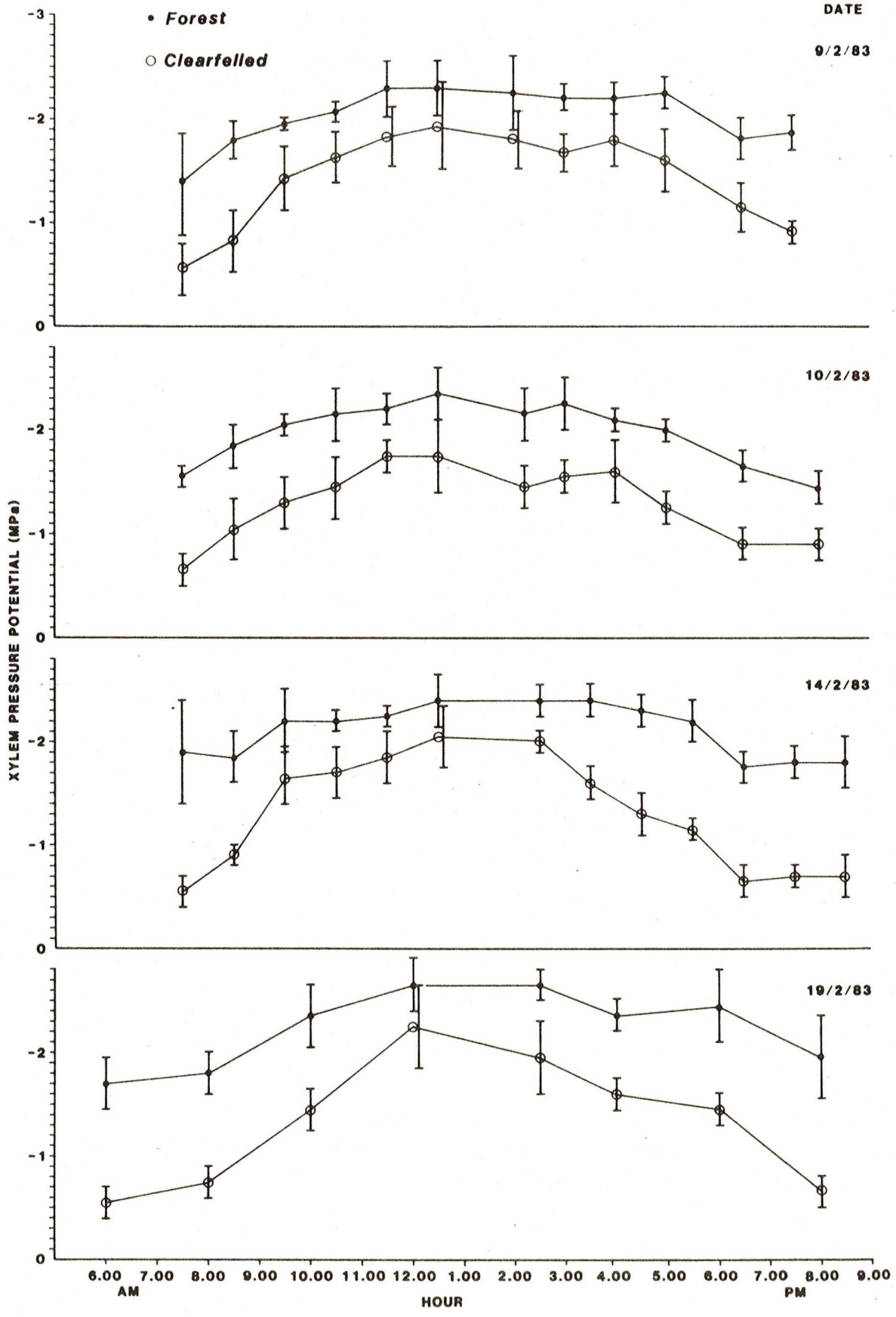
| | $\bar{x}$ S.E. |
|---|---|
| Forest with root competition | -1.8 ± 0.1 |
| Forest without root competition | -1.9 ± 0.4 |
| Forest with irrigation | -0.7 ± 0.1 |
| 100% canopy removal | -0.8 ± 0.2 |

TABLE 4.6

Mean and standard error stomatal resistance of advance growth beneath three levels of overstorey (0, 50 and 100%) during the middle of the day 19.2.1983.

| | | Stomatal Resistance $scm^{-1}$ | | |
|---|---|---|---|---|
| Time (DST) | | Forest | Shelterwood | Clearfell |
| 11.00 a.m. | $\bar{x}$ | 22.6 | 9.4 | 3.3 |
| | SE | ± 5.0 | ±1.3 | ±0.4 |
| | n | 10 | 10 | 10 |
| 4.00 p.m. | $\bar{x}$ | 27.8 | 10.6 | 5.9 |
| | SE | ± 3.5 | ± 1.3 | ±2.6 |
| | n | 10 | 10 | 10 |

Figure 4.16. Diurnal mean and 95% confidence interval for xylem water potentials for clearfell and forest advance growth during four days in February 1983.


• Forest
○ Clearfelled
DATE
9/2/83
10/2/83
14/2/83
19/2/83
XYLEM PRESSURE POTENTIAL (MPa)
-3
-2
-1
0
6.00 7.00 8.00 9.00 10.00 11.00 12.00 1.00 2.00 3.00 4.00 5.00 6.00 7.00 8.00 9.00
AM
HOUR
PM

## 4.5 DISCUSSION

In multi-aged E. delegatensis forests there is considerable spatial variation in the size and density of the even-aged regeneration. Biomass and density of the regrowth increase with distance from the surrounding overwood as canopy cover and litter mass decrease. The relationship between regrowth size and distance from mature trees has been reported for a number of different eucalypt forests (Opie, 1968, 1969; Incoll, 1979a; Rotheram, 1983) yet the physiological relationships of these patterns have not been established (Florence, 1971).

Eucalypt canopies do not cast deep shade over the forest floor. The forest at Waddamana was found to deplete 40-60% of the incoming solar radiation (Nunez pers. comm., 1983). In high rainfall areas dense closed-forests can develop beneath mature eucalypt canopies, and in more frequently burnt stands eucalypt regrowth can compete with the regenerating wet sclerophyll understorey species (Chapter 2). In the drier E. delegatensis forests dense understoreys do not develop and the eucalypt regeneration after fire is much slower growing than the regrowth in the wet forests (Chapter 2, Figure 2.4). The height of saplings in the forest at Waddamana is independent of the estimated summer and winter levels of solar radiation received by the advance growth. Rapid growth results from both trenching or fertilization of the regeneration in the forest.

Change in leaf morphology across the forest gaps may possibly be associated with the increased levels of radiation

over the gradient (Cameron, 1970). Within the dense stands of regrowth that develop in gaps there is some evidence that plant height is correlated with sky view factor. This relationship may possibly explain the asymmetrical form of the regrowth in the north-south plane where the tallest plants occur in the southern quadrant. An alternative,albeit unlikely (see below), explanation for this distribution could be the indirect effect of solar radiation on plant growth. Ashton and Willis (1982) suggest that increased soil temperatures following the creation of gaps in E. regnans forests may allow the development of a microflora that is favourable for healthy sapling growth. None of the above evidence supports the hypothesis that regrowth suppression is due to the shade from the mature forest canopy.

Chemical inhibition of the regeneration is another plausible hypothesis. At maturity several species of eucalypt have been shown to produce chemical substances which inhibit the development of germinates and seedlings of the same species, germinates of other species in the genus, and both Australian native and exotic understorey plants (Baker, 1965; del Moral and Muller, 1969, 1970; Al-Mousawi and Al-Naib, 1975; del Moral et al., 1978; and Ashton and Willis, 1982). Leachates from the canopy are an unlikely cause of suppression in the dry E. delegatensis forests because both saplings and seedlings growing beneath overwood showed significant increases in productivity following trenching. This conclusion is supported by the results of the bioassay which showed that leaf leachates caused no

inhibition of germinate growth. Similarly, the bioassay from the litter extract caused no inhibition in the development of the E. delegatensis germinates. However , the soil-cover pot experiment indicated that seedlings grown with a covering of litter were 89% of the size of plants grown with no covering and 83% of the height of plants treated with an inert mulch. This suppressive effect is small when compared to the massive differences in the size of the regrowth beneath the forest and in gaps. In nature this inhibitory effect would be slight as most of the forest litter would have been consumed in the fire that initiates seedling establishment (Chapter 3). Litter cover, bare soil and hessian mulch were not found to have any direct effect on the productivity of the advance growth although significant interactions between the above treatments and fertilization were revealed. The mulching effect of litter is clearly shown in this experiment where unfertilized plants grown with litter, litter and hessian and hessian had greater, albeit not statistically different ($P>0.05$), annual increments in height (6.3%, 6.5%, 7.9% respectively) than plants grown with no mulch (4.4%). Del Moral and Muller (1970) note the mulching effect of eucalypt litter and show that soil with a litter cover has a greater moisture content than that with none.

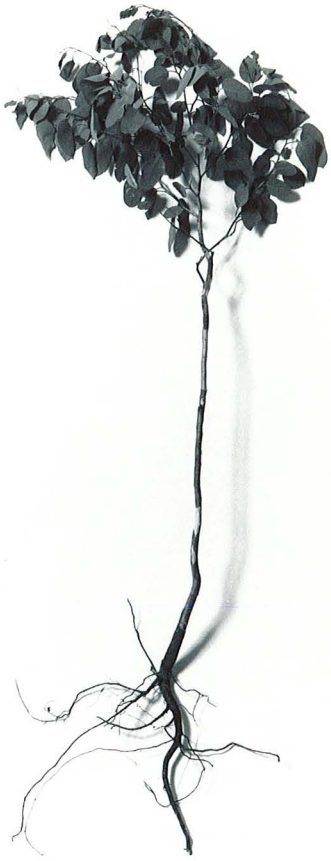
The dense and extensive root systems of mature E. delegatensis are largely confined to the top of the soil profile (Plate 4.3). The lack of deep sinker roots may be due to winter waterlogging of the subsoil (c. 60 cm) clay horizon (Ashton, 1975) which underlies the stoney mineral soil at Waddamana. The

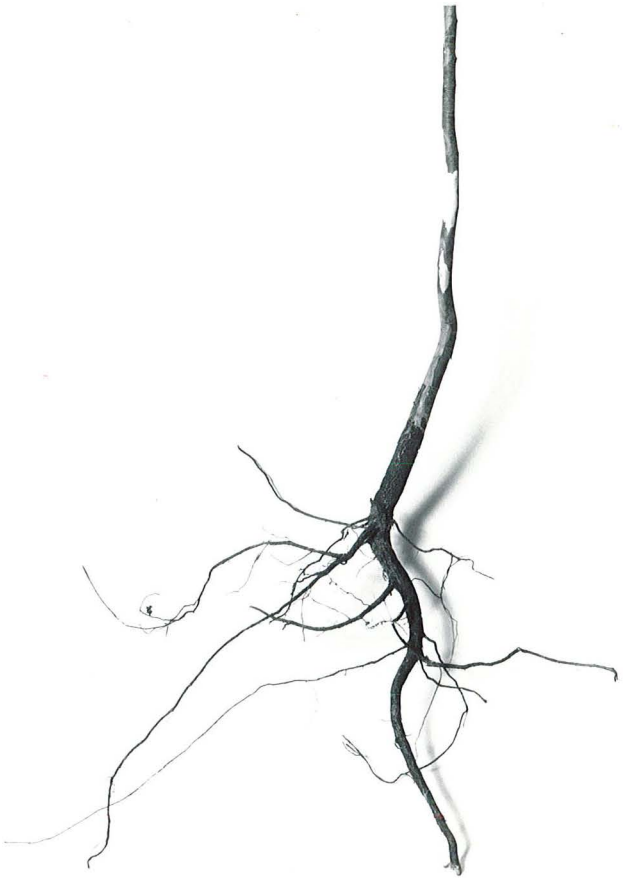
Plate 4.3. Shallow root plate of a wind thrown *E. delegatensis* tree on a partially logged site at Waddamana.

below ground biomass of E. regnans has also been shown to be mainly restricted to the surface soil horizons (Ashton, 1975; Incoll, 1979b). In this zone interspecific and intraspecific intermeshing of roots from different individuals is common (Chilvers, 1972; Ashton, 1975; Incoll, 1979b). The root systems of advance growth are characterized by a pronounced tap root which is surrounded by lateral roots which ramify both horizontally and vertically (Plate 4.4). The systems are also restricted to the top c 60 cm of the soil mantle. There is therefore a strong case to support the hypothesis that suppression is due to below ground competition.

Allelopathic exudates from plant roots have been suggested as an important cause of below ground competition (Story, 1967; Rovira, 1969; Robinson, 1970; Whitcomb, 1972). Root leachates from two north Australian rainforest trees, Grevilla robusta and Araucaria cunninghamii, have been shown to intraspecifically inhibit seedlings grown in otherwise optimal conditions (Webb et al., 1967; Bevege, 1968). In this study, leachates from freshly severed E. delegatensis roots were not found to inhibit germinate development, indicating that root toxins are not the cause of seedling suppression. Similarly, neither del Moral et al., (1978) nor Ashton and Willis (1982) were able to inhibit eucalypt seedling growth with leachates from cut roots. However, the latter authors conclude that on the basis of other experiments there is a case to support the hypothesis that exudates from living tree roots and their associated mycorrhizae may inhibit

Plate 4.4. Typical shoot and root development of a suppressed E. delegatensis plant. Height from stem base to growing tip 130 cm, tap root length 35 cm.





seedling growth in unburnt E. regnans forests. They concur with the findings of Florence and Crocker (1962) and Evans et al., (1967) that the root fungus Cylindrocarpon destructans is inhibitory to the normal development of eucalypt seedlings. Florence and Crocker (1962) demonstrated that fresh soil from wet forests was inhibitory to E. pilularis seedling growth while old soil was not. Ashton and Willis (1982) found that isolation of seedlings from root competition by trenching in E. regnans forests resulted in only limited improvement in their growth and survival. Given the rapid growth of E. delegatensis seedlings planted in forest soil that was isolated from root competition, it is unlikely that such rhizosphere antagonism is the major cause of the regrowth suppression. Similarly, seedling growth is not inhibited in the drier E. pilularis forest type (Cremer et al., 1978).

The severing of tree roots by trenching has long been known to cause marked changes in the composition and structure of forest understoreys (Fricke, 1904;Fabricius,1927,1929; Watt, 1931; Toumey and Kienholz, 1931;Watt and Fraser, 1933; Korstian and Coile, 1938;Lutz,1945). As in this study, Fricke (1904) Craib (1929) and Korstian and Coile (1938) found that trenching resulted in increased soil moisture and the authors concluded that root competition for water was the cause of the seedling suppression. However, Watt and Fraser (1933), who showed that the effect of trenching on a Pinus sylvestris woodland understorey was only partially replicated by nitrogenous fertilization and not at all by irrigation, have emphasised the

need for independent lines of evidence to determine the cause of plant responses to trenching.

The distribution of some eucalypt species has been shown to be correlated with variations in the soil nutrient status (Moore, 1959; Parsons and Specht, 1967; Parsons and Rowan 1968; McColl, 1969). Intense interspecific competition for nutrients is also well known in the genus (Moore, 1961; Parsons, 1968a; Burdon and Pryor, 1975). It is therefore possible that intraspecific competition for nutrients is the cause of the regrowth suppression. However this hypothesis is not supported by the uniformity of both the total and the available levels of nutrients in the forest and gap soils (Table 4.7). Similarly, foliar concentrations of all elements tested, other than nitrogen and sodium, were not correlated with the change in productivity (Table 4.8). Further, the foliage of the suppressed plants exhibited no symptoms of nutrient deficiencies (Will, 1961; Truman and Turner, 1972). Additions of fertilizer to planted eucalypts have been shown to induce significant increases in their productivity (Mitchell, 1966; Cromer, 1971; McIntyre and Pryor, 1974). This was observed in the growth response of the seedlings and advance growth. However the magnitude of the seedling response varied according to the presence or absence of root competition. (No similar experiments were conducted with the suppressed advance growth). Moisture availability was also shown to be greater in the trenched plots. The unfertilized-trenched seedlings were larger than the fertilized-untrenched seedlings,

TABLE 4.7

Soil pH, total and available soil nutrient concentrations in a forest gap stocked with healthy regrowth (figure 4.1).

| | | North | | | | South |
|---|---|---|---|---|---|---|
| | Distance (m) | 0-5 | 5-10 | 10-15 | 20-25 | 25-30 |
| Reaction | (pH) | 6.0 | 6.0 | 6.2 | 5.6 | 5.9 |
| Nitrogen | Total (%) | 0.14 | 0.10 | 0.14 | 0.15 | 0.20 |
| | Available (p.p.m.) | 110 | 84 | 84 | 99 | 99 |
| Phosphorus | Total (p.p.m.) | 180 | 310 | 250 | 190 | 160 |
| | Available (p.p.m.) | 5 | 8 | 3 | 9 | 11 |
| Potassium | Total (p.p.m.) | 180 | 230 | 190 | 160 | 190 |
| | Available (p.p.m.) | 65 | 30 | 35 | 60 | 50 |
| Calcium | Total (p.p.m.) | 1700 | 1800 | 1600 | 1080 | 1300 |
| | Available (p.p.m.) | 38 | 21 | 46 | 47 | 36 |
| Sodium | Total (p.p.m.) | 200 | 210 | 180 | 120 | 220 |
| | Available (p.p.m.) | 63 | 63 | 40 | 48 | 45 |
| Magnesium | Total (p.p.m.) | 560 | 720 | 500 | 340 | 530 |
| | Available (p.p.m.) | 6.0 | 2.5 | 11 | 10 | 8.0 |

TABLE 4.8

Tallest regrowth and foliar nutrient concentrations sampled in 2m wide belt transect across a gap.

| | North | | | | | | | South |
|---|---|---|---|---|---|---|---|---|
| Distance (m) | 0.5 | 5-10 | 10-15 | 15-20 | 20-25 | 25-30 | 30-35 | 35-45 |
| Regrowth height (m) | 1.2 | 1.3 | 2.9 | 1.7 | 6.4 | 7.3 | 7.2 | 2.5 |
| Nitrogen (%) | 1.0 | 0.9 | 1.1 | 1.1 | 1.3 | 1.2 | 1.1 | 1.2 |
| Phosphorus (p.p.m.) | 540 | 560 | 530 | 520 | 690 | 810 | 580 | 630 |
| Potassium (p.p.m.) | 3700 | 4600 | 3800 | 3400 | 4000 | 4800 | 4700 | 4700 |
| Calcium (p.p.m.) | 4800 | 7800 | 6700 | 3900 | 6200 | 7000 | 4900 | 4800 |
| Sodium (p.p.m.) | 83 | 98 | 97 | 69 | 98 | 110 | 94 | 73 |
| Magnesium (p.p.m.) | 2400 | 2500 | 2800 | 2600 | 2800 | 2200 | 2700 | 2000 |

suggesting that soil moisture rather than nutrients is critical in controlling seedling growth. After one year the fertilized-untrenched seedlings were also larger than the controls. This difference is probably due to accelerated growth during the wetter months of the growing season. This argument may also explain the response of the advance growth to the addition of nutrient but does not account for the lower growth rates of the fertilized-mulched stems when compared to those without soil cover. Further data are required to conclusively prove the hypothesis that the plant response to fertilizer is controlled by soil moisture availability. However on the basis of the above results there is a strong case to reject the hypothesis that regrowth suppression is due to intraspecific competition for nutrients. This conclusion is supported by the observation that on similar soils in high rainfall areas, dense understoreys and rapidly growing regrowth can develop beneath tall open E. delegatensis forest (Chapter 2, Figure 2.6).

It is well known that forests have drier soils than adjacent cleared areas (Fletcher and Lull, 1963; Ziemer, 1968; Troendle, 1970; Startz, 1972; Christensen, 1975; Johnston, 1975; Rogerson, 1976; Dunlap and Helms, 1983). In this study a steep moisture gradient from beneath the forest to the cleared area was detected. Surprisingly there was more moisture in the trenched plots with increasing distance from the overwood. This latter gradient is probably an artefact of the former because when the trenched plots were established the soils beneath the forest were significantly drier than those in the cleared area (Figure 4.13).

Alternatively the gradient may reflect spatial variation in rainfall interception across the transect.

Associated with the moisture gradient was a significant decline in seedling water stress. Similarly the advance growth on the clearfelled site was less drought stressed and was more productive than the controls beneath the forest. Dunlap and Helms (1983) have also found that tree competition for water resulted in suppressed growth of seedlings. Tree density has also been shown to be important in controlling plant water stress (Wambolt, 1973; Ashton et al., 1975; Dunlap and Helms, 1983). The variation in the stomatal resistance of the advance growth beneath the various levels of canopy removal supports this finding. The watered advance growth in the forest had low levels of drought stress similar to the plants on the clearfelled site. However, over the 10 weeks of irrigation, the watered plants in the forest did not respond by growing rapidly. McDonald (1976) found that Pinus ponderosa regrowth took up to four years to show a height growth response to overwood removal. He suggested that these plants first have to develop their root systems and photosynthetic area before they can increase in height. This suggestion also seems a reasonable explanation for the leaf area but not height increase of E. delegatensis advance growth in the 20 months after the removal of competition. On the basis of the above evidence it is concluded that E. delegatensis regrowth suppression is due to water stress. The slow growth rate and small leaf area appears to be an adaptive mechanism to survive

prolonged drought stress . The growth response of the advance growth to fertilization may result in increased drought damage during severe periods of water deficit, while the slower growing plants with their smaller leaf area may suffer less damage.

FOOTNOTE (1) Chemical composition of the fertilizer nitrogen; as nitrate 8.5%, as ammonium form 9.5%: phosphorus; as water soluble 2.1%, as citrate soluble 0.5%.: potassium; as potassium sulphate: sulphur as ; potassium sulphate 4.0%.

# CHAPTER FIVE

# MICROCLIMATE, REGENERATION HEALTH AND CANOPY COVER INTERACTIONS IN MULTI-AGED E. DELEGATENSIS FORESTS

## 5.1 INTRODUCTION

Mature E. delegatensis trees have been shown to have a strong suppressive effect upon the growth of the understorey regeneration. The complete absence of overstorey in some high altitude areas can also inhibit the growth of E. delegatensis regeneration. Hypotheses of the cause of "growth check" are equivocal although it is believed to be associated with the more frequent and severe frosts which follow canopy removal (Nunez and Sander, 1981, 1982; Webb et al., 1983; Keenan and Candy, 1984).

This chapter documents the different levels of damage to planted seedlings across a competition gradient and reports the microclimatic change on the forest floor following the removal of various amounts of canopy cover.

## 5.2 METHODS

The number of damaged and undamaged leaves (where damage was defined as >25% of leaf area killed) on the seedlings growing in each treatment across the trenched-untrenched transect (Figure 4.11) was recorded on the 8/7/1982, 11/1/1983 and 29/3/1983. On the last two measurement dates the number of plants with exposed roots was also noted. The sky view factor at each plot was measured using the methods described in Chapter 2.

The minimum surface temperature for 26 nights was recorded

for each plot over a one year period with triplicate maximum-minimum thermometers. These were located at ground level in a vertical position (the bulb was about 2 cm above the ground surface). At plots 1 and 6 on the transect the hourly mean soil ( c. 0.5 cm depth ) temperatures were measured with buried Campbell Scientific Inc. (CSI) 101 thermistor temperature probes and were recorded on cassette tape by a CSI CR21 data micrologger from 1/4/1983 until 17/8/1983. Hourly surface temperatures were added to these measurements from the period 18/8/1983 to 4/11/1983.

Prior to the removal of 0%,50% and 100% of the canopy in a small area (1.5 ha) at Waddamana the daily minimum forest floor temperatures were measured for 41 nights between 24/6/1981 and 14/11/1981. At each of the three sites (unlogged, shelterwood and clearfelled) 10 maximum-minimum thermometers were placed at regular intervals (c 20 m) along two 100 m transects which intersected at right angles. Following logging, the hourly mean ground temperature of the forest and clearfelled areas was measured from 14/8/1982 until 23/12/1982. The surface measurements were made with a spatially integrating 10 junction copper-constantan thermocouple network. The ten thermocouple junctions were evenly spaced over an area of about 100 $m^2$ and buried to a depth of 0.5 cm. The spatially integrated values were recorded on the CSI CR21.

On the 2/7/1982 and 9/7/1982 the predawn (c. 6.00 am) ground temperatures beneath a range of canopy covers were determined by

measuring at metre intervals on three (2/7/1982) or 10 (9/7/1982) belt transects with a Barnes infra red thermometer. The 30-50 m transects were run from the shelterwood to the clearfelled area. The location of each tree and stump on each site was determined from a 1m to 2 mm base map that was prepared by the CSIRO (Ellis pers. comm.,1981). The crown width of each tree was estimated trigonometrically.

## 5.3 RESULTS

At the beginning and middle of the 1982/83 growing season two way analysis of variance of the arcsine transformed data showed that there was a significant ($P<0.001$) gradient in leaf damage across the trenched-untrenched transect (Figure 5.1). The analyses also showed that at these dates there were significant interactions (8/7/1982 $P<0.01$, 11/1/1983 $P<0.001$) between the position and trenching treatments on the experimental transect. Analysis of variance revealed that transect position alone had a significant influence upon the proportion of the leaves which were damaged at the end of the growing season. The trenched seedlings at the cleared end of the transect had a greater number of leaves than the plants in all the other treatments on the transect (Figure 5.1). However these leaves were typically smaller and abnormally developed by comparison with the foliage on the plants growing in the other treatments (Plates 5.1 and 5.2 ).

The level of frost damage recorded for the plants protected from root competition for the first two sample dates was found to

Figure 5.1. Mean and 95% confidence interval of percentage leaf damage, and number of leaves for the seedlings in each treatment on the trenched untrenched transect at the middle of the 1982/83 growing season. The number of plants with frost-heaved root systems is also shown.

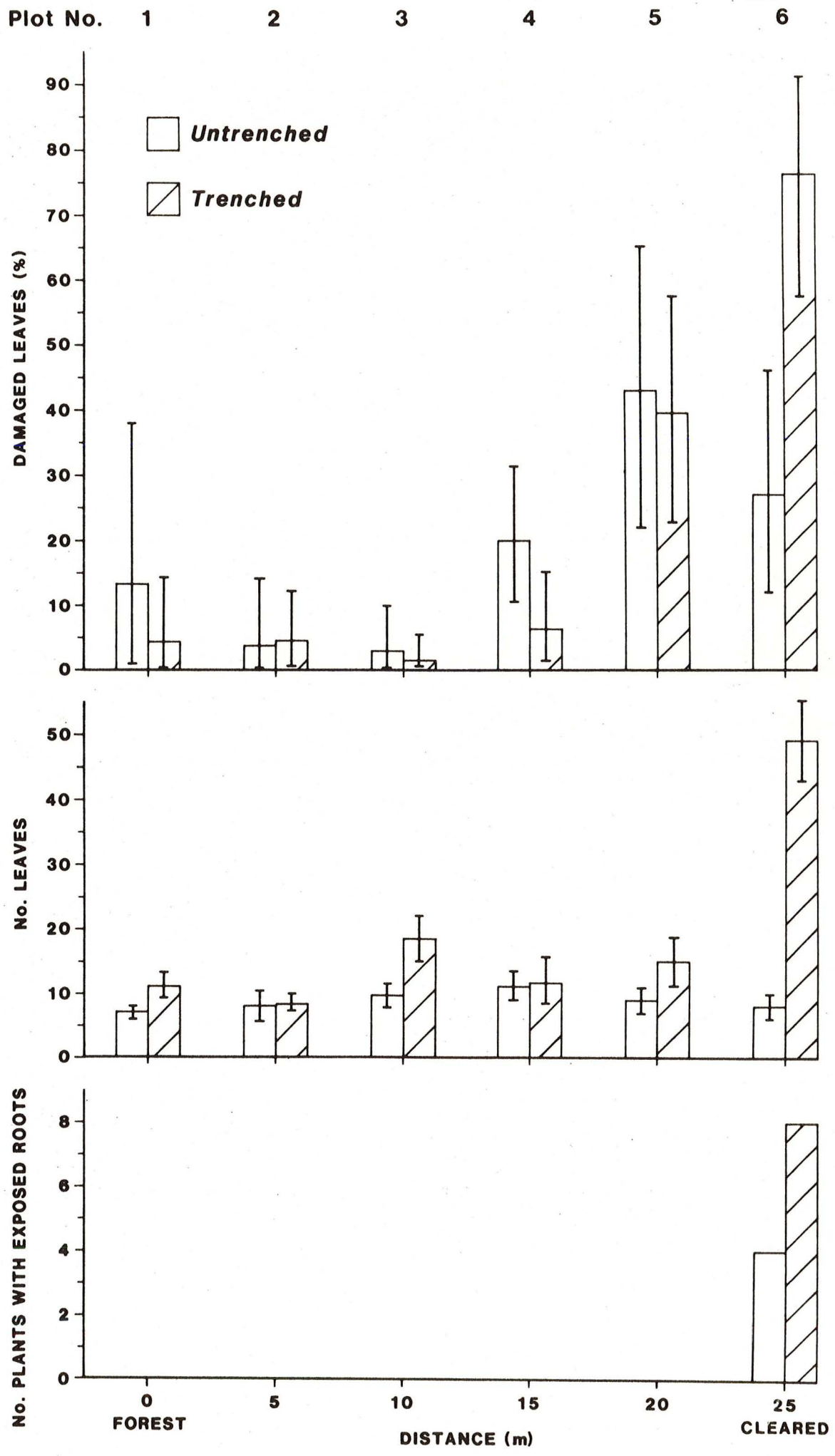

Plot No. 1 2 3 4 5 6
Untrenched
Trenched
DAMAGED LEAVES (%)
0
10
20
30
40
50
60
70
80
90
No. LEAVES
0
10
20
30
40
50
No. PLANTS WITH EXPOSED ROOTS
0
2
4
6
8
0
FOREST
5
10
15
20
25
CLEARED
DISTANCE (m)

Plate 5.1. Seedlings in the trenched and untrenched treatments at the forested end of the experimental transect.


Plot No 2
Trenched
15/2/83


Plot No 1
control

Plate 5.2. Seedlings in the trenched and untrenched treatments at the cleared end of the experimental transect.


Plot No 6
control
15/2/83


Plot No. 6
trenched

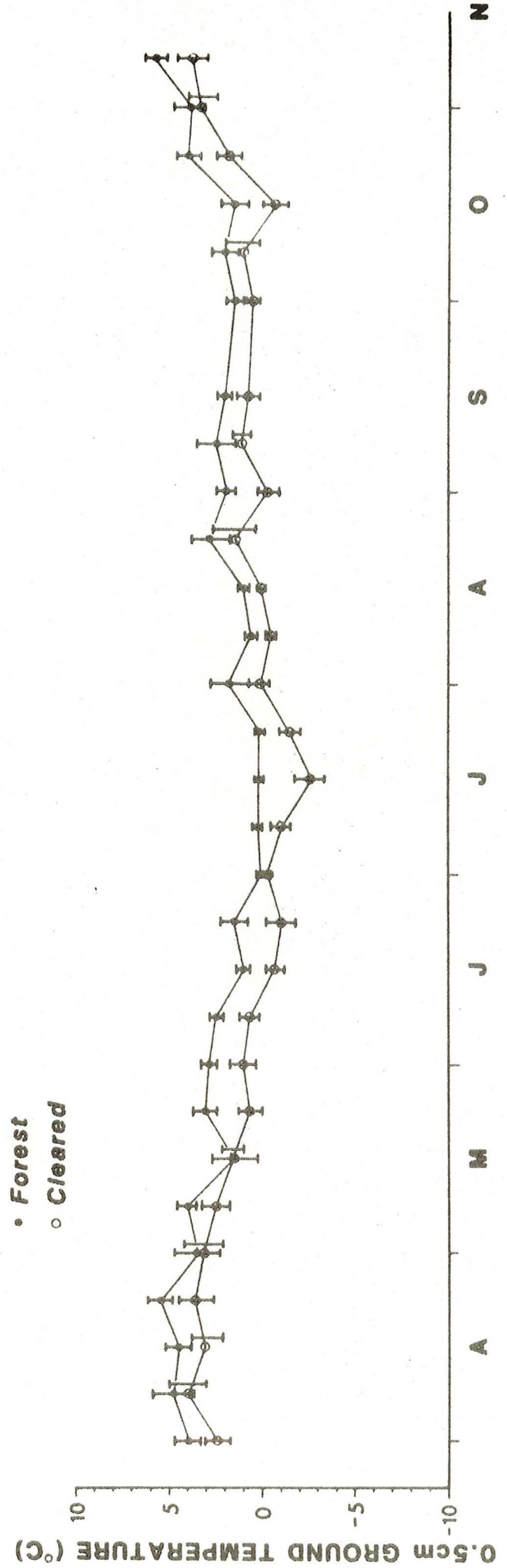
be significantly correlated to the sky view factor ($P<0.05$) and inversely correlated to the mean ($n=26$) minimum ground temperature ($P<0.05$) across the transect from the forest to the cleared area. The sky view factor and the mean minimum ground temperature across the transect were found to be highly correlated ($P<0.02$).

Plot six was the only position on the transect in which the root systems of some seedlings were partially heaved out of the soil (Figure 5.1). Figure 5.2 shows that the minimum mean hourly soil temperatures at this site were significantly ($P<0.001$) lower than those recorded beneath the adjacent (25 m) canopy. For nine weeks the weekly average minimum hourly temperature at the cleared end of the transect was below $0^{\circ}C$. In marked contrast, the weekly minimum soil temperature in the forest did not fall below freezing. The minimum subsoil temperatures at the cleared site are significantly ($P<0.001$) correlated with minimum ground surface temperatures, with the latter being consistently lower (Figure 5.3).

The mean ($n=41$) minimum ground temperatures of the clearfell and shelterwood areas prior from canopy removal were not statistically different to the mean minimum temperature of the forest floor. However following the removal of the canopy major changes occurred in the spatial pattern of frost. Measurements taken on (9/7/1982) show a $4^{\circ}C$ temperature gradient from the shelterwood to the cleared site (Figure 5.4). The isotherms are essentially orthogonal to the slope indicating that radiation

Figure 5.2. Mean and standard error of weekly minumum hourly average soil temperature at each end of the experimental transect. The sky view factors of plots 1 and 6 were 37% and 81% respectively.

Figure 5.3. Relationship between daily minimum hourly mean soil temperature and the surface temperatures for either end of the transect (n=71).


0.5cm GROUND TEMPERATURE (°C)
10
5
0
-5
-10
A
M
J
J
A
S
O
N
• Forest
○ Cleared

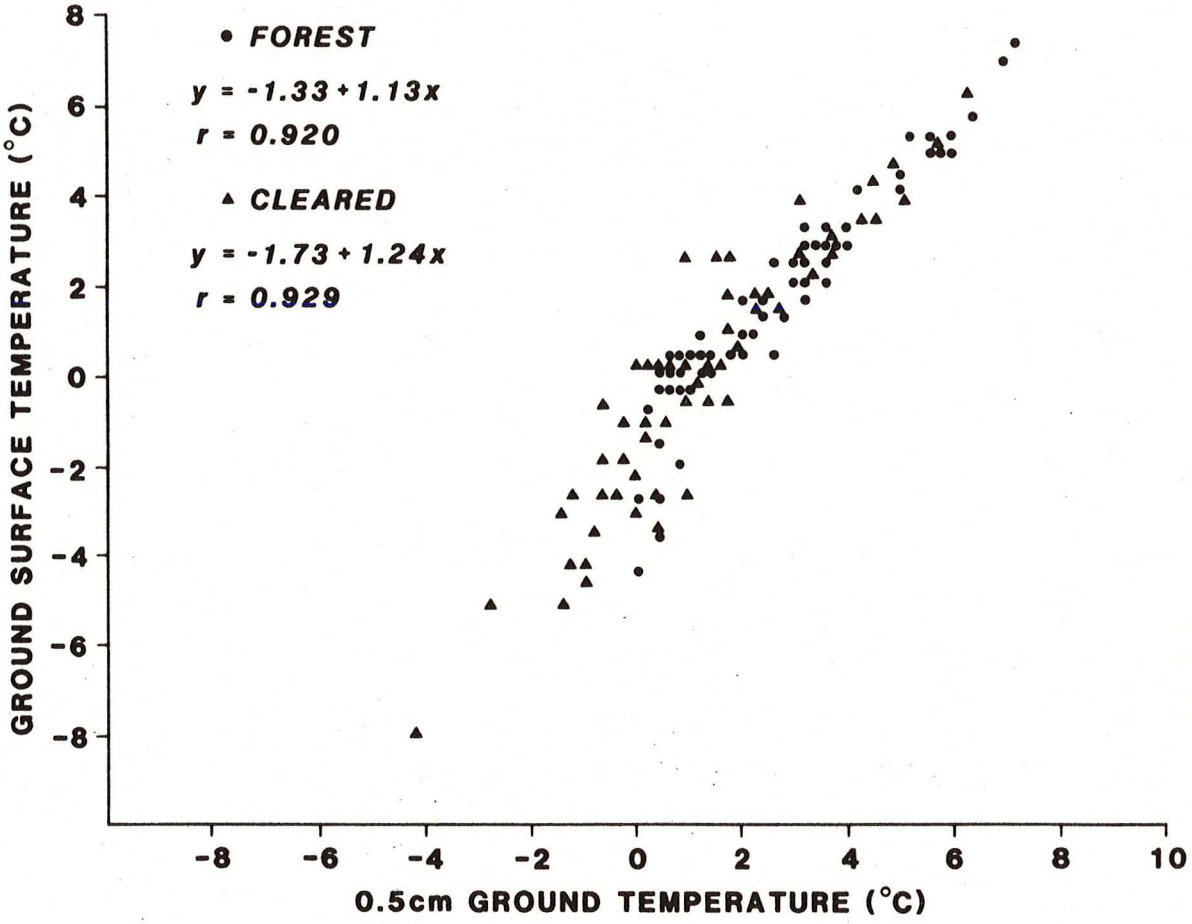
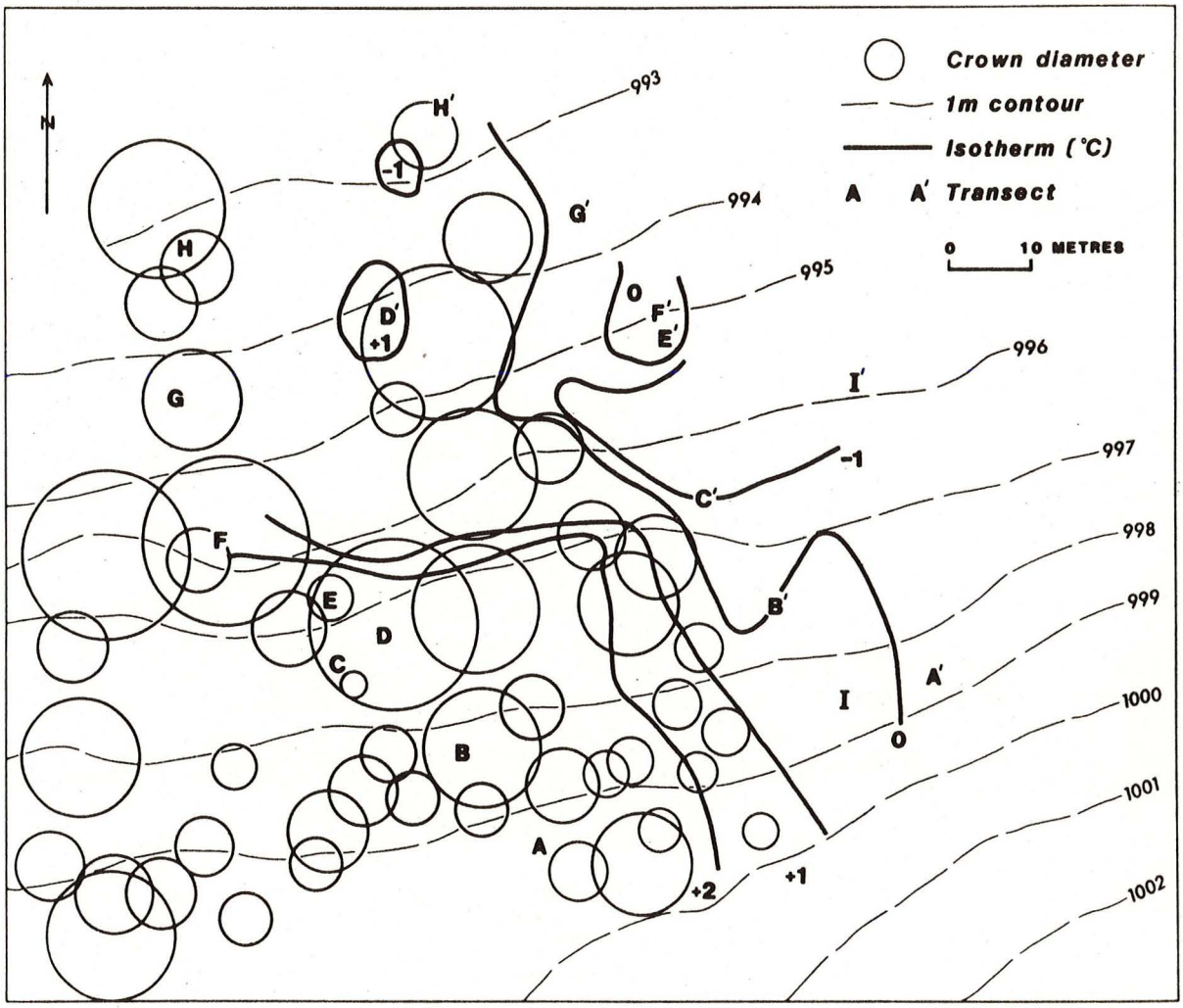

• FOREST
y = -1.33 + 1.13x
r = 0.920
▲ CLEARED
y = -1.73 + 1.24x
r = 0.929
GROUND SURFACE TEMPERATURE (°C)
0.5cm GROUND TEMPERATURE (°C)
8
6
4
2
0
-2
-4
-6
-8
-8
-6
-4
-2
0
2
4
6
8
10

Figure 5.4. Isotherm map of a frost in the clearfelled and shelterwood areas showing estimated position of each tree crown, location of the belt transects (AA′ to II′) and the 1 m contours. Temperature data were collected on the 9/7/1982 using a Barnes infrared thermometer.


Crown diameter
1m contour
Isotherm (°C)
A A' Transect
0 10 METRES
N
993
994
995
996
997
998
999
1000
1001
1002
H'
-1
G'
H
D'
+1
O
F'
E'
I'
G
-1
C'
F
E
D
C
B'
B
I
A'
O
A
+2
+1

rather than cold air drainage is critical to the development of ground frost. The effect of canopy interception of long wave radiation is clearly shown in Figure 5.5 where the mean surface temperature of each 5 m section of the 10 belt transects is significantly correlated ($P<0.01$) to the mean distance to the nearest tree crown. The complete removal of canopy cover produces a microclimatic regime that has greater range of temperatures, with lower minimum and greater maximum mean hourly temperatures, than the forest (Figure 5.6). In no week did the mean hourly minimum surface temperature in the forest fall below freezing, while the coldest mean hourly surface temperature on the clearfelled site was -6°C. The clearfelled site also had a greater number of hours per day when the mean surface temperature was greater than or equal to 10°C, indicating that it may have a growing season of longer duration than the unlogged site (Figure 5.7).

## 5.4 DISCUSSION

The health of the regrowth in the forest gaps suggests that, following the selective logging, the regeneration suffered little or no significant frost damage The clearfelled and unlogged sites had a mean difference in daily minimum hourly ground surface temperatures of 3.6°C (SE 0.2°C) between August and December 1982; a result similar to the 4°C difference between the partially logged area and the clearfelled site (Figures 5.4 and 5.6). Therefore it is probable that the microclimate of small gaps is similar to that of unlogged forest. However, there is insufficient data for an exact quantification of the relationship with gap size and frost severity.

Figure 5.5. Relationship between mean distance to the nearest tree crown and each ground temperature class for the frost in the clearfelled and shelterwood area. Data derived from Figure 5.4.

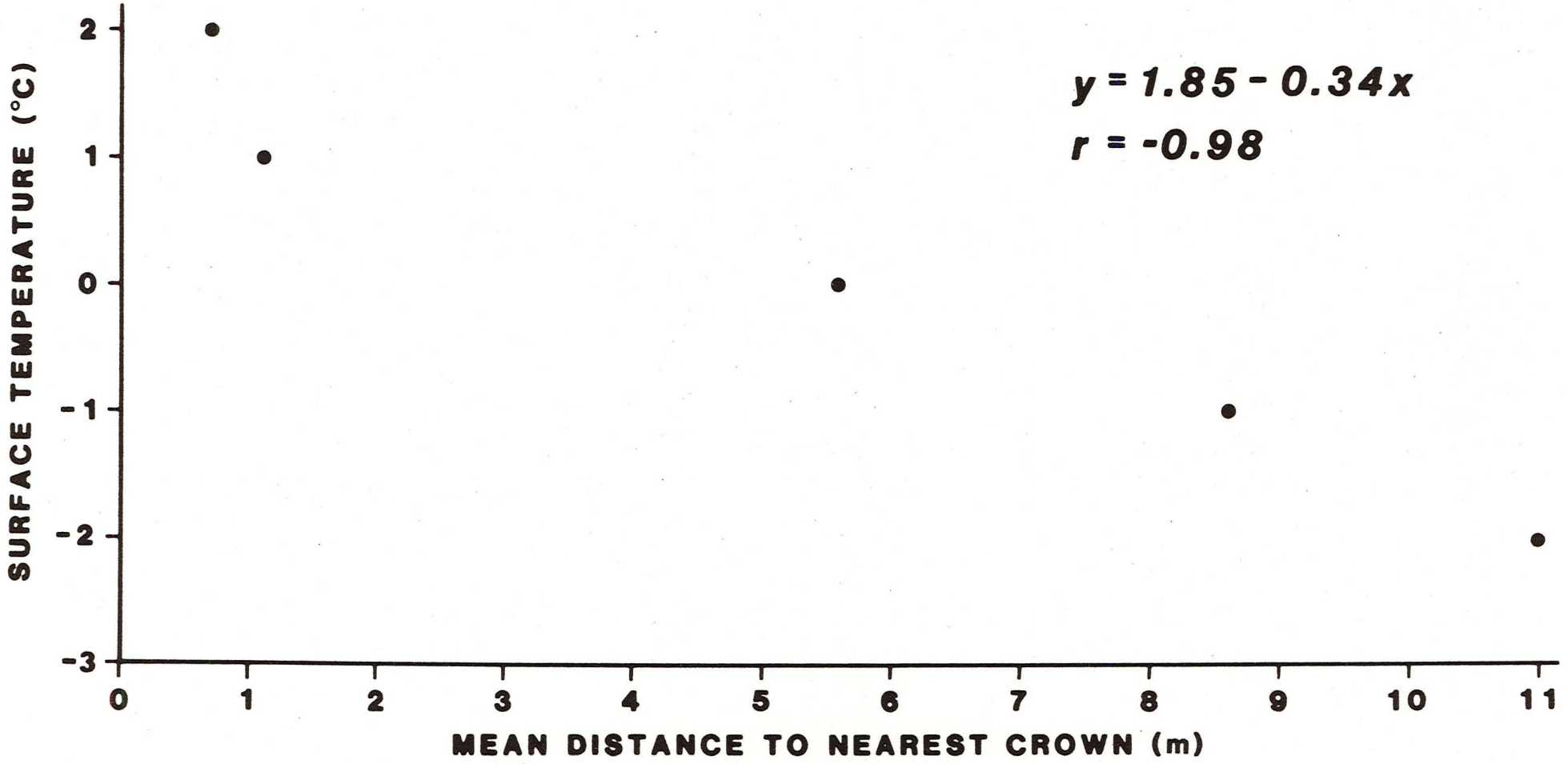

y = 1.85 - 0.34x
r = -0.98
SURFACE TEMPERATURE (°C)
2
1
0
-1
-2
-3
0
1
2
3
4
5
6
7
8
9
10
11
MEAN DISTANCE TO NEAREST CROWN (m)

Figure 5.6. Mean and standard error of weekly maximum and minimum average hourly ground temperature in the forest and clearfell sites from August to December 1983.The weekly minimum average hourly temperatures are also shown.

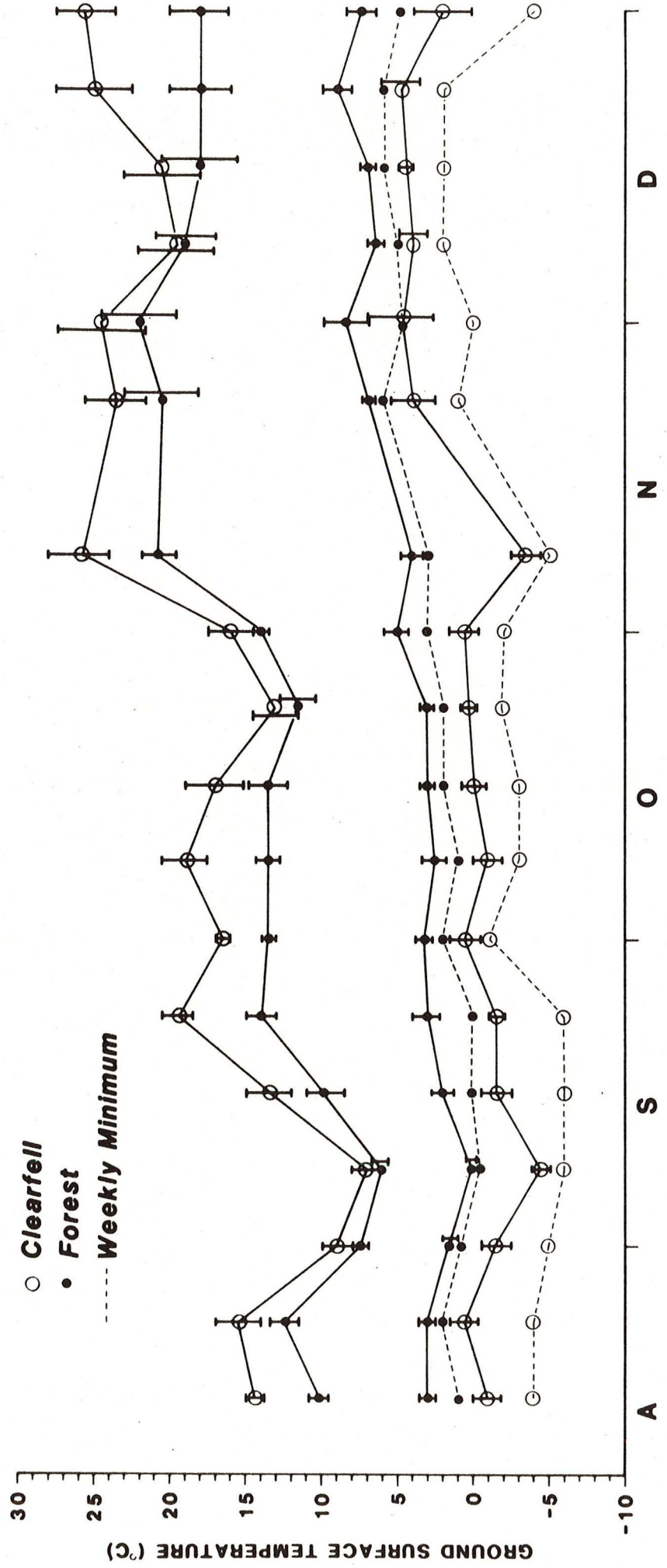
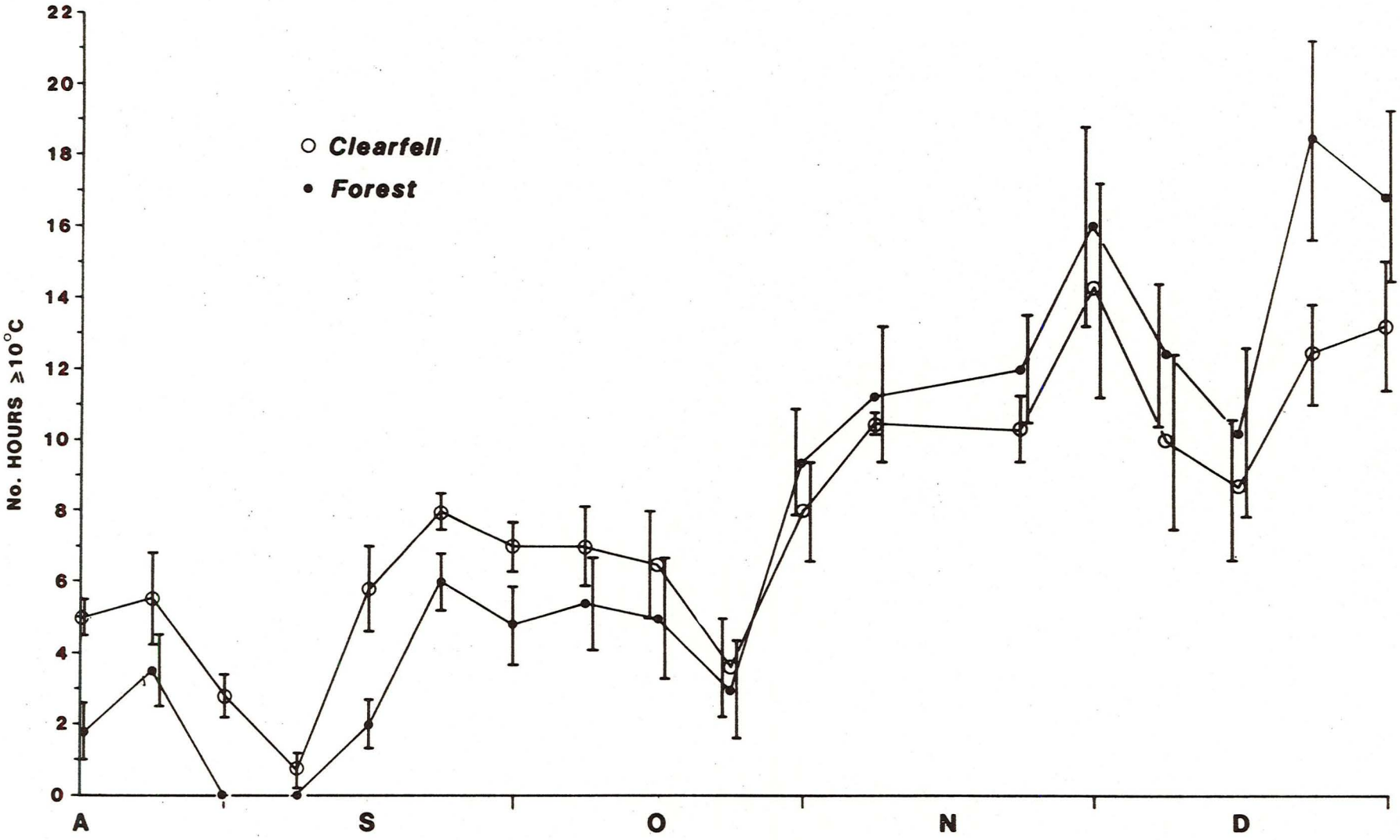

GROUND SURFACE TEMPERATURE (°C)
30
25
20
15
10
5
0
-5
-10
A
S
O
N
D
○ Clearfell
• Forest
Weekly Minimum

Figure 5.7. Mean and standard error of the number of hours per day where the surface temperature is greater than or equal to 10°C in forest and clearfelled sites.


22
20
18
16
14
12
10
8
6
4
2
0
No. HOURS ≥10°C
○ Clearfell
• Forest
A
S
O
N
D

Forested areas have been generally recorded to have higher nocturnal temperatures than adjacent cleared land (Day and Peace, 1946; Smith, 1970; Geiger, 1971; Dale, 1972; Williamson and Minore, 1978; Hungerford, 1979; Riefsnyder, 1982). Nunez and Sander (1982) found that unlogged and partially logged central Tasmanian E. delegatensis stands (Figure 2.1, site 22) were 2°C and 4°C warmer at night than an adjacent clearfelled area. They found that although canopy cover significantly reduced longwave radiation loss, minimum air temperature was also significantly correlated with topographic elevation. They concluded that both advection and radiation processes were involved in frost formation. This does not appear to be the case at Waddamana, given the direct relationship between canopy cover and ground temperature on the slightly sloping experimental site (Figures 5.4 and 5.5). Radiation loss is therefore considered the predominant factor in frost formation at the Waddamana experimental site. This conclusion is supported by the finding that an adjacent knoll, the only area of elevated topography near the experimental site, was found to cool at the same rate as the lower cleared area (Nunez pers. comm., 1983).

Although there are numerous reports of the interspecific and intraspecific frost tolerance of Eucalyptus (Pryor, 1956; Ashton, 1958; Boden, 1958; Sherry and Pryor, 1967; Eldridge, 1968; Green, 1969; Paton, 1972, ,1980,1981;Thomas and Barber,1974; Awe and Shepherd, 1975; Kirkpatrick, 1975; Heavilin, 1978; Harwood, 1980, 1981; Rook et al., 1980; Webb et al., 1983) the impact of canopy

removal on eucalypt regeneration is poorly understood. Barber (1955) noted that E. delegatensis regrowth suffered greater damage following a December frost in logged areas than in unlogged areas. Grose (1960a) found than frost heave of roots was a more important factor than foliage damage in controlling E. delegatensis establishment on logged sites. At Waddamana seedlings at the cleared end of the transect suffered both root heave and heavy foliar damage. Differences, between observations in Victoria and Tasmania may be due to genotypic variation in frost tolerance of E. delegatensis (Webb et al., 1983). The advance growth was not found to suffer any frost damage following canopy removal (Chapter 4). This difference in frost tolerance may be due to physiological changes associated with age (Paton, 1981). The above differences may also be explained by the relationship between the vertical temperature profile and topography. Nunez and Sander (1981) found that on clear nights the minimum temperature occurred c. 5.0 cm above the near level surface at their clearfelled site and was between 0.5°C and 2°C colder than the ground. These inversions are believed to be strongly associated with radiative cooling rather than advective processes (Oke, 1970). Such a temperature profile would account for the differences in damage between the seedlings and the advance growth. The E. delegatensis forests studied by Grose (1960a) are on steep valley slopes where advection processes would predominate. The above argument may explain the spatial variation in the health of E. delegatensis regeneration following clearfelling (growth check). Keenan and Candy (1984) found that

stunted regeneration were correlated to poorly drained sites which are also subject to cold air drainage. The development of a deep layer of cold air would cause the slow growth of E. delegatensis regeneration until it could overtop the frost layer. This notion is supported by the observation of Keenan and Candy (1984) that healthy regrowth on check prone sites often have extremely twisted lower stems. In South African E. fastigata plantations Sherry and Pryor (1967) found that frost damage was inversely related to both topographic position and stem height. They suggest that at the foot of the slope the fastest growing genotypes escaped frost damage in their second winter by overtopping the layer of cold air accumulation. Similarly the maintenance of subalpine inverted treelines has also been shown to be related to severe advection frosts which develop in flat bottomed valleys. Gradients of 10°C have been reported across the eucalypt woodland - grassland ecotone with extreme minima falling below 15°C in most winters (Farrell and Ashton, 1973; Moore and Williams, 1976; Harwood, 1976). On these valley floors eucalypts are typically unable to overtop the frost layer and remain stunted bushes (Farrell and Ashton, 1973).

These results suggest that regeneration on clearfelled plateau sites is more likely to suffer severe frost damage than seedlings on steep slopes. Frosts are less severe on slopes than on level ground because of the downward flow of cold air. Given the predominance of radiative cooling on level ground, frost severity can be controlled by canopy cover. Small gaps, with low sky view factors, created by the partial logging did not result

in increased frost severity. However, the complete removal of the canopy led to significantly lower minimum ground temperatures. The relationship between eucalypt canopy cover and minimum temperature (Figure 5.5) suggests that there is also a relationship between the diameter of clearings and frost severity. This relationship has been noted elsewhere (Geiger, 1971, figure 189) but requires more detailed investigation for eucalypt forests.

# CHAPTER 6

# CONCLUSION

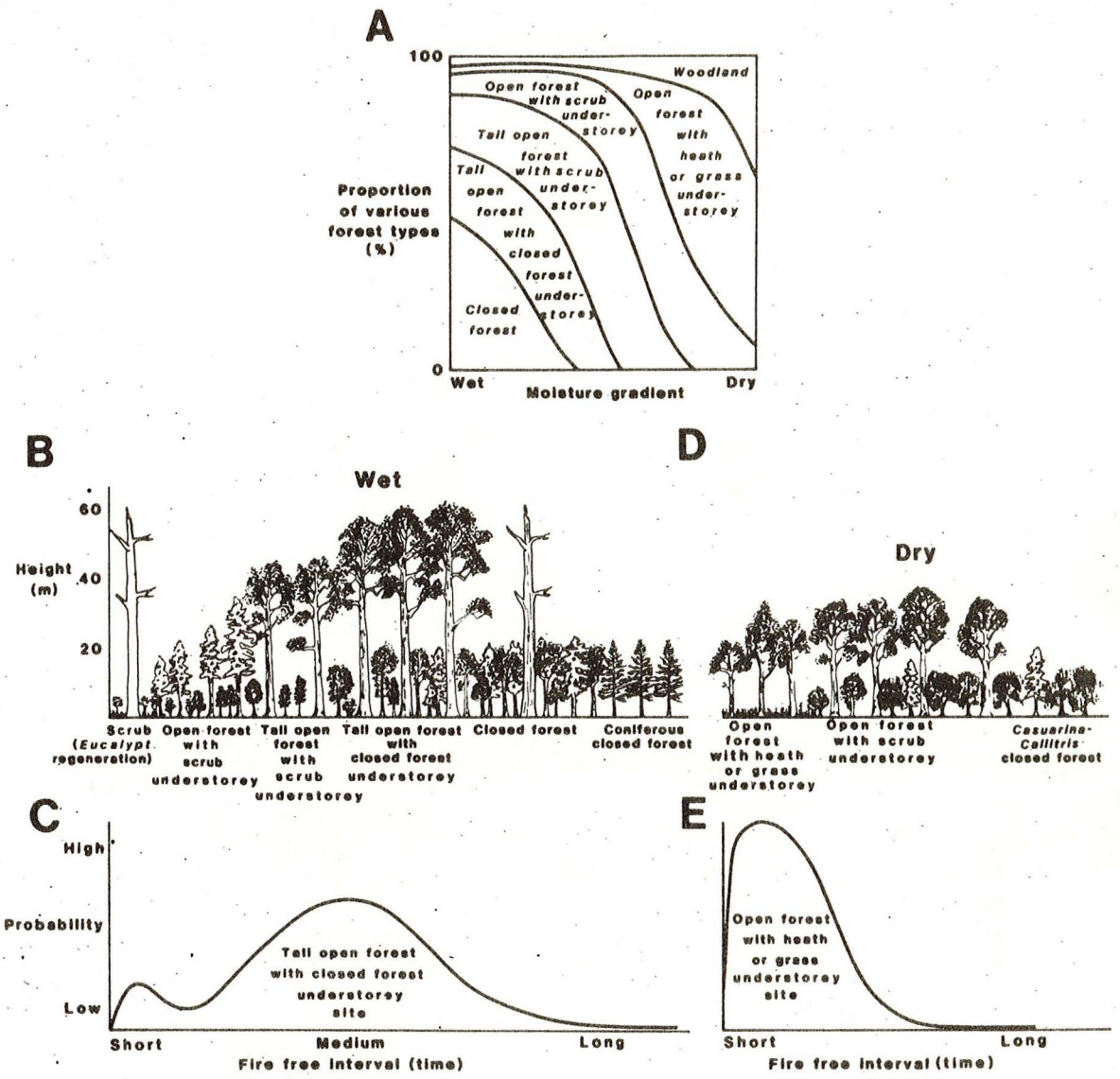
## 6.1 INTRODUCTION

Most silvicultural studies of eucalypt regeneration have been restricted to tall open-forests (e.g. Ashton, 1956; Gilbert, 1959; Cunningham, 1960; Grose, 1960a; Cremer, 1964). The paucity of knowledge concerning open-forest regeneration processes in lower rainfall areas has been highlighted by the current debate over appropriate methods of logging and regeneration of these communities (Bowman and Jackson, 1981; Felton, 1982; Jackson and Bowman, 1982; Kirkpatrick and Bowman, 1982; Felton and Lockett, 1983). This concluding chapter discusses the results of this thesis in relation to contemporary models of natural and artificial eucalypt regeneration.

## 6.2 NATURAL REGENERATION

Figure 6.1 provides a theoretical synthesis of Tasmanian eucalypt forest regeneration processes. Diagram A suggests that the structure of eucalypt forest varies with the amount of available moisture. This model is supported by the results of chapter two which showed that understorey type and stand height are highly correlated to annual rainfall. The diagram also shows that forests typical of low rainfall areas can occur in wet areas. This skewed distribution of forest types has been interpreted as evidence of the influence of fire on understorey vegetation (Jackson, 1968). This conclusion is supported by Figure 2.9 which demonstrates the correlation between the last regeneration event and the scatter in the high rainfall *E. delegatensis* forest

Figure 6.1. Theoretical synthesis of Tasmanian forest regeneration processes. Diagram A shows the skewed distribution of forest types over the rainfall gradient. Diagrams B and C hypothesize that wet eucalypt forests are even-aged fire seres. There is believed to be a relatively long time interval between successive fires. Diagrams D and E also suggest that dry eucalypt forests are seral, but unlike wet forests they are multi-aged and highly adapted to the frequent incidence of fire (Jackson, 1965, 1968; Mount, 1979; Harris and Kirkpatrick 1982; Kirkpatrick and Dickinson, 1984; personal observation).


A
100
0
Proportion of various forest types (%)
Wet
Moisture gradient
Dry
Woodland
Open forest with scrub understorey
Open forest with heath or grass understorey
Tall open forest with scrub understorey
Tall open forest with closed forest understorey
Closed forest
B
Wet
Height (m)
60
40
20
Scrub (Eucalypt regeneration)
Open forest with scrub understorey
Tall open forest with scrub understorey
Tall open forest with closed forest understorey
Closed forest
Coniferous closed forest
D
Dry
Open forest with heath or grass understorey
Open forest with scrub understorey
Casuarina-Callitris closed forest
C
High
Probability
Low
Tall open forest with closed forest understorey site
Short
Medium
Long
Fire free interval (time)
E
Open forest with heath or grass understorey site
Short
Long
Fire free interval (time)

understorey vegetation ordination scores.

Because of the influence of fire frequency upon forest type, no precise climatic limit to wet forest distribution can be determined, even for geographically disparate slopes with similar aspect, although the 750 to 1000 mm isohyets are sometimes used (Bowman and Jackson, 1981; Kirkpatrick, 1981). However, the epithets "wet" and "dry" refer to the type of understorey rather than to the climate of the stand (Beadle and Costin, 1952).

Diagrams B and C (Figure 6.1) hypothesize that wet and dry eucalypt forests are fire seres. For example, given a fire free interval the senescent wet eucalypt forest would be replaced by temperate rainforest species that, unlike eucalypts, are able to regenerate beneath dense understoreys and in small canopy gaps (Gilbert, 1959; Jackson, 1968). Dense understoreys are infrequently dry enough to carry fire (Figure 6.1 C) but when they burn the stand is believed to be killed in an intense conflagration (Jackson, 1968). The stand is then replaced by an even-aged crop of tree and shrub seedlings that grow rapidly on the ashbed (Mount, 1979). Jackson, (1968) suggested that, if a fire occurs in the highly inflammable eucalypt heath and scrub before the maturity of the regrowth (Figure 6.1 C), the ensuing regeneration on the site would be dominated by treeless vegetation. In this study temperate rainforest understoreys were found to develop beneath the long unburnt stands of E. delegatensis (Figures 2.2 and 2.4) but, in contrast to the above model, no stand was uniform in age. Therefore a fire prior to

the maturity of the eucalypt regrowth would not cause the elimination of the eucalypts from the site but would result in a more open, fire adapted understorey type (Figure 2.9; Ashton, 1981).

In lowland areas that are too dry for rainforest or broad-leaf shrub understories Casuarina and/or Callitris may displace eucalypts in the absence of fire ( Figure 6.1 D and E; Withers and Ashton, 1977; Harris and Kirkpatrick 1982). The climax species in low rainfall high altitude forests are unknown. The potential climax species may be either extinct or restricted to moister and/or fire protected habitats (as suggested for areas of the Australian mainland by Singh et al., 1981).

Jacobs (1955) has proposed a model, since elaborated by Mount (1979), that emphasizes the dependence of eucalypt regeneration upon the very frequent fires presently typical of the dry sclerophyll forest environment (Figure 6.1 E and Table 2.4). The model suggests that recruitment of seedlings into the multi-aged stand occurs following the creation of a gap, and the locally intense fire which is fuelled by the smashed crown of the fallen tree. Mechanical failure is attributed to repeated butt damage from the combustion of litter and limbs which accumulate at the base of the stem. Mount (1979) stresses the importance of intense fire for the successful establishment of eucalypts. He suggests that they continue to grow rapidly if "other conditions are suitable", otherwise becoming suppressed lignotuberous seedlings that may be released following further disturbance.

Chapters two and three have demonstrated the almost total dependence of the natural regeneration of E. delegatensis upon fire. Similarly the surveys in chapter three support the notion that gap formation follows frequent fire damage to the butts of trees (Plate 3.1). However the seedbed studies showed that E. delegatensis, like most other eucalypts, readily establishes on mechanically disturbed seedbeds in the absence of fire (Chapter 3).

The studies by Parsons (1968b) in semi-arid mallee eucalypt forests concur with the conclusion of chapter three which showed that spring and summer rainfall is critical in controlling the density of germinates on disturbed soils. Further, Zimmer (1940) and Parsons (1968b) suggest that the successful establishment of mallee germinates is dependent on increased soil moisture caused by reduced transpiration following the death or defoliation of the overwood by fire. Such increase in soil moisture following defoliation by fire in heath or ringbarking of E. obliqua forest has been reported by Specht et al., (1958) and Hopkins (1964) respectively. In mallee forests Parsons (1968b) suggests that, when the overwood recovers, most of the fire-stimulated regeneration is killed through intraspecific competition for moisture. The remainder grows into suppression unless tree death creates a gap in the stand. These suppressed lignotuberous seedlings form a pool of regeneration that can grow rapidly by utilizing surplus soil moisture made available by further disruption of canopy transpiration. Such dynamic development of suppressed seedlings following the removal of overwood

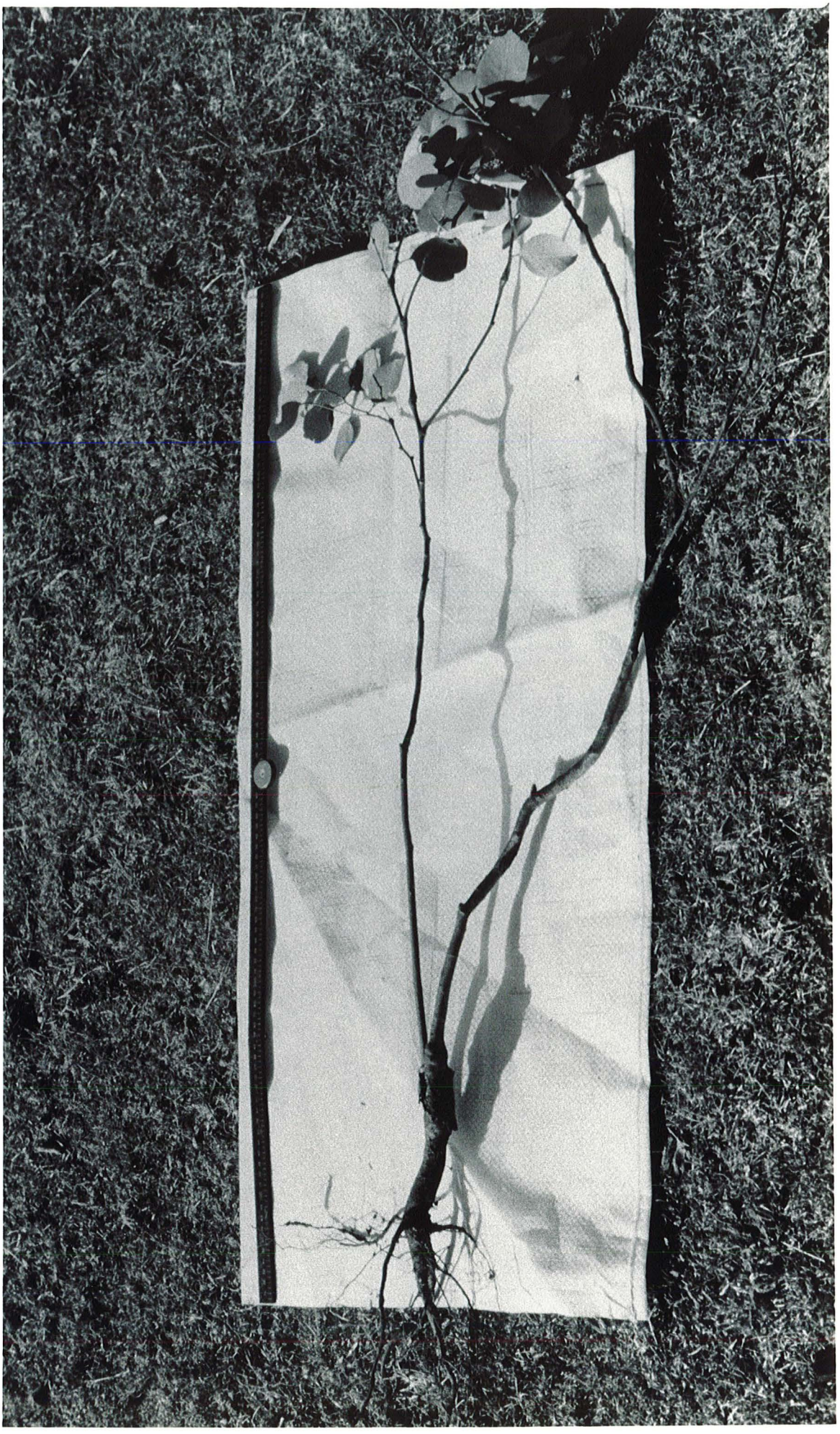
competition through logging (van Noort, 1960; Henry and Florence, 1966; Curtin and King, 1979; this study), death of overwood (van Noort, 1960) or defoliation by burning (Henry and Florence, 1966), has been reported in a number of different dry eucalypt forests. Van Noort (1960) suggested that seedling growth response is due to reduction in intraspecific competition for moisture, but Henry and Florence (1966) and Florence (1971) hypothesize that the maintenance of the suppressed condition is due to direct competition between the overwood and regeneration for something other than water or nutrients. The results of the experimental studies clearly show that E. delegatensis germinates, seedlings and advance growth are suppressed by intraspecific competition with the overwood for soil moisture. Henry and Florence (1966) note that the response to overwood removal is dependent upon the size of the gap. Similarly, it has been observed that most isolated small diameter stumps formed by past selective logging of dry E. delegatensis forests are not surrounded by dense regrowth, while larger gaps in which several stems have been logged, are heavily stocked. The surplus soil moisture following the removal of a small tree may be completely used by the surrounding overwood to support rapid growth, whereas their root systems are unable to fully exploit larger gaps. In nature, gaps are usually created following the mechanical failure of repeatedly damaged butts with large basal areas. In this study, the smallest basal area of a stump in a heavily stocked selectively logged gap was 0.57 $m^2$. The minimum amount of basal area that must be removed from a stand to stimulate dense

regrowth requires further investigation.

Goodwin (1984) has demonstrated that past selective logging of multi-aged tall open E. delegatensis forest resulted in a significant increase in the annual diameter increment of the surrounding overwood. Similar increases in tree ring width corresponding to past selective logging have been observed on the stumps of recently clearfelled dry E. delegatensis forests. It is likely that the rapid growth of trees following selective logging in both wet and dry forest is due to increased availability of soil moisture.

Suppressed E. delegatensis saplings are extremely fire sensitive and therefore, unlike most other eucalypt advance growth, their potential for opportunistic dynamic development is restricted to the fire free interval. A small proportion of the burnt advance growth was found to resprout, and a similar proportion of advance growth plants were observed as having dead stems with healthy basal resprouts in the unburnt forest at Waddamana (Plate 6.1). Lignotuberous-like swellings have been infrequently observed on the carrot-like taproot and are also reported by Boland et al., (1980b) as occasionally occurring on advance growth sampled at several Tasmanian locations during a study of the species geographic variation. It is not known whether these swellings are associated with vegetative recovery, and if they are, whether they are an atavism of a lignotuberous habit or selection towards that condition. While the suppressed advance growth is unlikely to survive fire, the released saplings

Plate 6.1. Vegetative recovery of a suppressed *E. delegatensis* advance growth plant collected from the unburnt forest at Waddamana.



have a higher likelihood of survival because of their thick fibrous bark and canopy height above the inflammable open heath understorey and litter layer. Fire appears to thin the heavily stocked gap regrowth, where the dominant stems have the greatest chance of survival.

This suggests that the fire free interval is critical in controlling recruitment into the stand. For example, if the interval is less than the time required for seedlings in gaps to become fire resistant through height growth and the development of thick fibrous bark, then a stand would probably become understocked. Evidence for this hypothesis is that, associated with the decline of the Tasmanian hunter-gatherers, who are believed to have practiced widespread and frequent burning (Jones, 1969), are peaks of tree recruitment into dry forests and the absence of any recruitment into some wet forests (Figure 2.2).

Frost does not appear to be an important factor in the natural regeneration of E. delegatensis forests. Chapter five showed that the creation of gaps through partial logging had little effect upon the minumum ground surface temperature. The health of the regeneration in gaps created by past selective logging is further evidence to support this conclusion. However, seedlings on level ground without canopy shelter suffered severe frost damage. Whether seedlings that arise after severe crown fire on level topography suffer similar damage is unknown. The poor health of regeneration under some ringbarked E. delegatensis

forests on the Central Plateau of Tasmania (e.g. Barren Tier near Shannon, Figure 2.1) suggests that naked crowns provide little shelter. However, crown damaging fires are exceptional and the fire resistant habitat of Tasmanian E. delegatensis quickly produces replacement crown cover.

In a recent review, Whitmore (1982) has argued that forests throughout the world are fundamentally similar in their mode of regeneration. He notes that gaps of various sizes are created in all forest types through allogenic or autogenic disturbance. He suggests that large gaps are dominated by tree species that are dependent upon high levels of solar radiation for growth, while shade tolerant species are able to successfully colonize small gaps. This generalization may be suitable for the description of regeneration processes in wet eucalypt forest or the climax temperate rainforest (Gilbert, 1959) but it is not appropriate for the dry eucalypt communities. Gap phase replacement has been shown to be related to available soil moisture rather than to solar radiation in these fire-dependent forests.

## 6.3 ARTIFICIAL REGENERATION

Forest harvest and regeneration schedules form a continuum from massive clearfelled coupes where kilotonnes of logging debris are consumed in intense regeneration fires to single tree selection systems. Table 6.1 summarizes the attributes of three subjectively defined groups of silvicultural systems that have been used in eucalypt forests. The two major distinguishing features of each group are the area of forest made devoid of

TABLE 6.1

Principal attributes of three subjectively classified groups of silvicultural systems used in eucalypt forests. Information derived from: Jacobs, 1955; Cunningham, 1960; Grose, 1960b; Needham, 1960; Frankcombe, 1961; Dexter, 1967; Florence *et al.*, 1970; Felton and Cunningham, 1971; Florence and Phillis, 1971; White, 1971; White and Underwood, 1974; Schuster, 1980; Bowman and Jackson, 1981; unpublished summaries supplied by the Tasmanian Forestry Commission, Forests Commission Victoria, Department of Forestry Queensland, and the company Forest Resources Tasmania; unpublished management plans from the Forestry Commission of N.S.W.; and observation of silvicultural practice in Victoria, N.S.W., Western Australia and Tasmania.

| Variable | Category | Intensive logging | Partial logging | Selective logging |
|---|---|---|---|---|
| Forest Type | Wet forest | X | X | X |
| | Dry forest | X | X | X |
| Mean size of clearings within management unit | > 1.0 ha | X | | |
| | 0.1 - 1.0 ha | | X | |
| | < 0.1 ha | | X | X |
| Criteria for selecting harvested stems | Merchantability | X | | X |
| | Maturity | | | X |
| | Diameter | | | X |
| | Density | | X | |
| | Basal area | | X | |
| Principal reason for retaining stems | Shelterwood | | X | |
| | Seed trees | | X | |
| | Growth potential | | X | X |
| | Culls | X | | |
| | Aesthetics | | X | |
| Fate of unwanted stems | Left standing | X | X | X |
| | Fallen to waste | X | X | X |
| | Killed | X | X | X |
| Mode of seedbed preparation | Hot slashfire | X | X | |
| | Top disposal fire | X | X | X |
| | Mechanical disturbance | X | X | X |
| | Logging disturbance | X | X | X |
| Principal source of regeneration | Aerial sowing | X | X | |
| | Manual sowing | X | X | X |
| | Heads | X | X | X |
| | Overwood | X | X | X |
| | Overwood induced | X | X | |
| | Advance growth | X | X | X |
| Next logging activity initiated when: | Regeneration established | | X | |
| | Regeneration healthy | | X | |
| | Retained stems merchantable | | X | X |
| | Regeneration merchantable | X | | |
| Structure of forest when regeneration is mature | Even-aged | X | X | |
| | Multi-aged | | | X |

TABLE 6.2

Variation of logging practice in *E. delegatensis* forests within and between the three subjectively derived groups of silvicultural systems.

| | Name of system | Location and forest type | Mode of Selection of harvested stems | Treatment of cutover stand/ seedbed preparation | Mode of regeneration | Aim of system | Reference |
|---|---|---|---|---|---|---|---|
| INTENSIVE LOGGING | Clear-felling | Victorian Alps wet forests | Log all merchantable trees, unless marked for retention, to lowest possible basal area. Growing stock may be preserved in groups if present. | Fell or poison any overwood in excess of $7m^2/ha$. Burn slash and/or mechanically disturb. | Artificial seeding or planting. | Supply sawlog, increase forest productivity, conserve allocated growing stock. | For.Com.Vic. (pers.comm., 1982) |
| | Clear-felling | Northwestern Tasmanian wet forests | Log all merchantable trees. | Mechanically disturb by bulldozing understorey. | Seed from fallen tree crowns. | Supply sawlog and pulpwood | Needham (1960) |
| | Clear-felling | Eastern Tasmanian dry forests | Log all merchantable trees | Slash-burn 80% of cutover sites; unburnt sites only where well stocked with advance growth. Kill culls which compete with regeneration. | Aerial sowing of seed from species native to area and seed from culls. Some advance growth and coppice on unburnt sites. | Produce even-age productive stand for pulpwood at a cutting cycle of about 50 years. | Felton and Cunningham (1971) Bowman and Jackson (1981) |

(contd.) 2/..

TABLE 6.2 (contd)

PARTIAL LOGGING

| Name of system | Location and forest type | Mode of selection of harvested stems | Treatment of cut stand/seedbed preparation | Mode of regeneration | Aim of system | Reference |
|---|---|---|---|---|---|---|
| Seedtree | Victorian Alps, wet forests | Log 70% merchantable stems. | Mechanically disturb seedbed; salvage-log retained stems 3-4 yrs after first cut. | Natural seedfall from overwood. | Supply sawlog and utilise natural seedfall. | Grose (1960b) |
| Potential sawlog retention | Eastern Tasman-Tasmanian dry forests | Log 1-3ha patches, removing all old growth (>110 yrs old) in integrated operation. Mark regrowth (<110 yrs old) in cut-over patch for removal, leaving potential sawlog trees. Mark damaged regrowth for removal after above operation. | Burn slash in cool fire. | Natural seedfall from overwood. | Conserve vigorous sawlog growing stock and concurrently supply pulpwood and sawlog. | For.Com.,Tas. (pers.comm., 1981) |
| Potential sawlog retention | Northeastern Tasmanian dry forests | Retain trees between 25-60 cm d.b.h. with good stem form and healthy crowns. All other trees, except culls, cut in an integrated sawlog-pulpwood operation. Retained trees: cut either in, between or at the beginning of the next cycle. | Burn slash in cool fire (optional) | Natural seedfall from overwood and unburnt fallen crowns, with or without light aerial sowing (0.5 kg/ha). Some advance growth and coppice on unburnt sites. | Retain trees which are currently pulpwood but have potential as sawlog. | For.Com.,Tas. (pers.comm., 1981) |
| Partial cutting | Central Tasmanian dry forests | Retain all trees below 68cm d.b.h. Integrated sawlog-pulpwood harvest of all other stems. | Burn slash in cool fire (optional). | Natural seedfall from overwood and unburnt fallen crowns, with hand-seeding of landings and snig tracks. Aerial seeding if natural crop is inadequate. Some advance growth and coppice on unburnt sites. | Retain potential sawlog, improve the long-term productivity of selectively logged forests. | Forest Resources (pers.comm., 1981) |

(Contd) 3/..

TABLE 6.2 (contd)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| PARTIAL LOGGING | Shelterwood | Northeastern Tasmanian wet forests | Retain about 50% of canopy cover. Tree retained chosen for large crowns, even spatial distribution, and balanced retention/ removal of pulp and sawlog. | Burn slash in cool fire (optional). Leave culls standing after second cut unless suppressing regeneration. Second cut occurs when regeneration is well established (possible 5-10 yrs after first cut). | Natural seedfall from overwood and unburnt fallen crowns, with or without light aerial seeding (0.5 kg/ha). | Provide regeneration shelter from frost. | For.Com.,Tas. (pers.comm., 1981) |
| | Shelterwood | Central Tasmanian dry forests | Retain all potential sawlog to 70 cm d.b.h. plus additional stems of good form to give 10 stems/ ha. minimum. Log all other trees in integrated pulp/sawlog operation. Minimise damage to existing growth. | Mechanically disturb. Burn slash in cool fire (optional). Remove shelter stems when mature sawlog size. | Natural seedfall from overwood and unburnt fallen crowns. Light aerial seeding (0.5 kg/ ha) if required. Enrichment planting of high quality site areas with *E. nitens* and *E.delegatensis*. Some advance growth and coppice on unburnt sites. | Maintain multi-aged stands for supply of sawlog and pulp within 20 yrs of treatment. Assist regeneration on exposed sites by provision of shelter. | Forest Resources (pers.comm., 1981) |
| | Shelterwood | Central Tasmanian dry forests | Remove best sawlog thin stems of poor form with no sawlog potential. Retain approx. 50% of dominant stems. Remove scattered overmature stems where feasible. | No burning, mechanical disturbance if rquired. | Natural seedfall from overwood and fallen crowns. Some advance growth and coppice on unburnt sites. | Promote sawlog for future cut. | Forest Resources (pers.comm., 1981) |

(contd) 4/..

TABLE 6.2 (contd)

SELECTIVE LOGGING

| Name of System | Location and forest type | Mode of Selection of harvested stems | Treatment of cutover stand/seedbed preparation | Mode of regeneration | Aim of system | Reference |
|---|---|---|---|---|---|---|
| Selective sawlogging | Southeastern N.S.W. Dry forests | Retain merchantable trees from cutting on the basis of conserving vigor, reducing defect, eliminating expected mortality, and providing regeneration. If insufficient vigorous trees available for seed, retain wind-firm trees at a spacing no greater than 80m. | Remove nonmerchantable trees remaining after logging where they interfere with growth potential of retained stems. Burn slash in cool fire and/or mechanically disturb. | Natural seedfall from overwood and unburnt fallen crowns. Planting if above unsuccessful. | Maintain fully stocked forest with vigorous trees for sawlog supply. | For.Com.,N.S.W. (1980) |
| Sawlog group selection | Northeastern Tasmanian dry forests | Log small groups of sawlog trees. | Burn slash in cool fire. | Natural seedfall from overwood and fallen unburnt crowns. Some advance growth and coppice on unburnt sites. | Minimize the aesthetic impact of forestry operation adjacent to a national park. | For.Com.,Tas. (pers.comm., 1981) |
| Sawlog group selection | Central Tasmanian dry forests | Log 40% sawlog trees. | Mechanically disturb. Burn slash in cool fire (optional). | Natural seedfall from overwood and fallen unburnt crowns. Some advance growth and coppice on unburnt sites. | Supply sawlogs until integrated logging operations allow the utilization of pulpwood. | For.Com.,Tas. (pers.comm., 1981) |
| Sawlog group selection | Central Tasmanian dry forests | Log sawlog trees >68cm. d.b.h. | Mechanically disturb. Burn slash in cool fire (optional). | Natural seedfall from overwood and fallen unburnt crowns. Some advance growth and coppice on unburnt sites. | Supply sawlogs | For.Com.,Tas. (pers.comm., 1981) |
| Integrated selective logging | Central Tasmanian dry forests | Log stems with no growth potential as pulp or sawlog. | Mechanically disturb. Burn slash in cool fire (optional). | Natural seedfall from overwood and unburnt crowns. Some advance growth and coppice on unburnt sites. Hand sowing if necessary. | Provide shelter for frost prone sites and maintain growing stock for future cutting cycles. | Forest Resources (pers.comm., 1982) |

trees through logging within the cutting unit and the age structure of the regenerated stand. Table 6.2 illustrates the variety of methods of logging and regeneration of E. delegatensis forests within and between the subjectively defined groups.

The clearing of large tracts of forest (c. 100 ha), burning of unused timber and other logging slash, and aerial sowing of seed native to the area was first developed in Victorian wet E. delegatensis forests (Grose et al., 1964) and is the system used in almost all Tasmanian forests. Large coupes and slash burning have been shown to be used for economic and fire management considerations rather than ecological necessity (Raison, 1980; Bowman, 1981; Bowman and Jackson, 1981) given that eucalypts in wet and dry forests readily establish on seedbeds of mechanically disturbed mineral soil (Chapter 3). However the extraction of timber with modern machinery resulted in only a small amount (c. 10%) of disturbance to the stony soil at Waddamana (Chapter 3). Bulldozers could produce and have produced suitable seedbeds, but these machines are economically less efficient than the currently favoured rubber tyre skidders. Given the widespread use of skidders by timber contractors, cool fire is probably the only practical way of preparing a suitable seedbed. This method suffers the disadvantage of killing most of the advance growth that survives logging but may result in less soil erosion than mechanical disturbance. The decision to burn clearly depends upon the density of advance growth and the area of disturbed soil on the cutover site. Aerial sowing is not mandatory for the production of an even-aged crop of regeneration. A range of

partial logging systems, which retain seedtrees at various densities until their seed is shed or the regeneration established, have been used either experimentally (Cremer, 1960; Cunningham, 1960; Grose, 1960b; Frankcombe, 1961), or prior to the widespread use of aerial sowing (Florence ,1964 ;Cremer, 1971) or during shortages of bulk seed (Korven-Korpinen and White, 1972) and are currently used in Western Australia and Victoria (White and Underwood, 1974; Table 6.2) to regenerate wet eucalypt forests. Intense slash fires can be used in such seedtree systems but are unsuitable for other partial logging systems (i.e. potential sawlog retention and shelterwoods) because of the risk of damaging the retained trees (Jackson and Bowman, 1982). The main weakness with partial logging systems is the potential for destroying the established regeneration when the overwood is removed in the second cut. This problem is particularly acute in shelterwoods where the second logging is delayed until the regeneration is considered immune from the effects of frost, and in heavily stocked potential sawlog systems where logging is delayed until the retained stems are merchantable. The results of regeneration surveys following the felling of overwood in shelterwoods are unavailable (Forestry Commission, Tasmania, pers. comm., 1981). In the absence of data the assessment of damage to 12 year old *E. delegatensis* regeneration following pulpwood removal in a previously selectively logged wet forest by the Tasmanian Forestry Commission suggests that overwood removal, if carefully conducted, does not cause unacceptable damage to regrowth

(Goodwin, pers. comm., 1981).

Unlike the above systems, selective logging maintains a multi-aged forest. Given that some wet forests are multi-aged, it is possible for these stands to be managed by selective logging (Jacobs, 1955; White and Underwood, 1974). However most foresters consider selection an inappropriate method for tall open eucalypt forests (Gilbert and Cunningham, 1972; White and Underwood, 1974) The Australian group selection system whereby small groups of trees are logged and even-aged regrowth fills the canopy gap has had a long history in dry eucalypt forests (Jacobs, 1955). Originally, merchantable stems were selected by sawmillers, but in an attempt to preserve growing stock for further cutting cycles, government forest agencies imposed a set stem diameter below which no merchantable tree could be logged (Jacobs, 1955). Florence (1970), Florence et al., 1970 and Florence and Phillis (1971) have discussed the productivity of the eastern coast forests on the mainland of Australia that have been managed for sawlog production by diameter limit cutting. They formed the general conclusion that the system was silviculturally disappointing because of the high retention of substandard stems and the poor response of the suppressed trees to overwood removal. Goodwin (1984) however has shown that E. delegatensis is able to grow rapidly following selective logging. Removal of inferior trees can be achieved through the application of morphological criteria rather than arbitrary stem diameter specifications (Florence et al., 1970; Florence and Phillis,

1971). Given available pulpwood markets, stems that are not of sawlog quality can also be used rather than cut to waste.

Intensive logging of E. delegatensis forests on plateau sites is likely to result in regeneration that suffers severe frost damage (Webb et al., 1983; Keenan and Candy, 1984). Shelterwoods are the currently preferred alternative, because like intensive logging systems, they produce discrete units of even-aged regeneration. The arguments for and against the conversion of multi-aged forests into even-aged stands have been discussed by Kirkpatrick and Bowman (1982). They concluded that on the basis of the available information clear felling might be less expensive in the short term . However,in the medium term, selection may be an economically superior system as it allows the maturation and harvesting of stems retained for their growth potential at the initial logging. They also suggested that multi-aged forests are more resistant to the destructive effects of wildfire. This suggestion is supported by the results of chapter three which showed that E. delegatensis trees are fire resistant while the non-lignotuberous regrowth, especially the small plants with thin bark, was extremely fire sensitive. Clearly both selection and shelterwoods are more expensive in the short term than clearfelling as the partial and selective logging systems require greater planning and supervision and considerable care by the contractors in avoiding damage to regeneration and retained trees. The relative difference in cost between partial logging and selective logging is unknown as is the difference in administrative efficiency. Similarly the differences in

productivity between even and multi-aged stands is unknown (Kirkpatrick and Bowman, 1982). Although shelterwoods may have the presumed advantage of producing a more easily managed stand of even-aged regrowth, the system has the same disadvantages as intensive logging : diminished aesthetic and nature conservation values, greater risk of soil erosion and losses in productivity following wildfire . However , densely stocked shelterwoods may significantly reduce soil erosion when compared to more heavily cut partially logged sites with low levels of canopy cover. Past selective logging in high altitude E. delegatensis forests have produced dense stands of healthy regrowth in forest gaps.

Given the currently available pulpwood markets there is the opportunity to realize the ideal form of the Australian group selection system where only the stems with no further potential for growth are removed from each size class (Jacobs, 1955). This system is well suited to the fire and frost prone dry E. delegatensis forests that have been shown to maintain an irregular age structure through gap phase replacement. The optimal size of gaps and the ideal stocking of stems in each size class requires further investigation.

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# APPENDIX

| SPECIES AND AUTHORITY | FAMILY |
|---|---|
| *Acacia dealbata* Link. | Mimosacaea |
| *A. melanoxylon* R. Br. | Mimosaceae |
| *A. mucronata* Willd. | Mimosaceae |
| *A. verniciflua* A. Cunn. | Mimosaceae |
| *Anopterus glandulosus* Labill. | Escalloniaceae |
| *Araucaria cunninghamii* Ait.ex.D.Don | Araucariaceae |
| *Athrotaxis selaginoides* D.Don | Taxodiaceae |
| *Banksia marginata* Cav. | Proteaceae |
| *Bedfordia linearis* DC. | Compositae |
| *B. salicina* DC. | Compositae |
| *Callitris* Vent. | Cupressaceae |
| *Cassinia aculeata* R. Br. | Compositae |
| *Casuarina* L.ex.Adan. | Casuarinaceae |
| *Coprosma hirtella* Labill. | Rubiaceae |
| *C. quadrifida* (Labill.) Robinson | Rubiaceae |
| *C. nitida* Hook f. | Rubiaceae |
| *Cyathodes glauca* Labill. | Epacridaceae |
| *C. parvifolia* R. Br. | Epacridaceae |
| *C. pendulosa* S.J.Jarman | Epacridaceae |
| *Cylindrocarpon destructans* (Zins.) Scholten | Hyphomycetes (class) |
| *Eucalyptus brookerana* A.M.Gray | Myrtaceae |
| *E. coccifera* Hook.f. | Myrtaceae |
| *E. dalrympleana* Maiden | Myrtaceae |
| *E. delegatensis* R.T. Baker | Myrtaceae |
| *E. fastigata* Deane et Maiden | Myrtaceae |
| *E. globulus* Labill. | Myrtacaea |
| *E. gunnii* Hook.f. | Myrtaceae |
| *E. obliqua* L'Hérit | Myrtaceae |
| *E. pilularis* Sm. | Myrtaceae |
| *E. regnans* F. Muell. | Myrtaceae |
| *Gaulthera hispida* R.Br. | Ericaceae |
| *Gonocarpus humilis* Orchard | Haloragaceae |
| *Grevillea robusta* A. Cunn. | Proteaceae |
| *Hakea lissosperma* R.Br. | Proteaceae |
| *Helichrysum dendroideum* N.A.Wakefield | Compositae |
| *Helichrysum hookeri* (Sond.) Druce | Compositae |

| Species and Authority | Family |
|---|---|
| *Leptospermum lanigerum* (Ait.) Druce | Myrtaceae |
| *Lissanthe montana* R. Br. | Epacridaceae |
| *Lomatia tinctoria* R. Br. | Proteaceae |
| *Notelaea ligustrina* Vent. | Oleaceae |
| *Nothofagus cunninghamii* (Hook) Oerst. | Fagaceae |
| *Olearia argophylla* F. Muell. | Compositae |
| *O. erubescens* (DC.) Dippel | Compositae |
| *O. lirata* (Sims.) Hutch. | Compositae |
| *O. phlogopappa* (Labill.) DC. | Compositae |
| *O. stellulata* (Labill.) DC. | Compositae |
| *O. viscosa* (Labill.) Benth. | Compositae |
| *Phebalium squameum* (Labill.) Druce | Rutaceae |
| *Phyllocladus asplenifolius* (Labill.) Hook.f. | Podocarpaceae |
| *Pimelea drupacea* Labill. | Thymelaeaceae |
| *P. nivea* Labill. | Thymelaeaceae |
| *Pinus ponderosa* Laws. | Pinaceae |
| *P. sylvestris* L. | Pinaceae |
| *Pittosporum bicolor* Hook. | Pittosporaceae |
| *Pomaderis apetala* Labill. | Rhamnaceae |
| *Prostanthera lasianthos* Labill. | Labiatae |
| *Pteridium esculentum* (Forst.f.) Nakai | Dennstaedtiaceae |
| *Pultenaea juniperina* Labill. | Papilionatae |
| *Tasmania lanceolata* (Pair.) A.C.Sm. | Winteraceae |
| *Telopea truncata* (Labill.) R. Br. | Proteaceae |
| *Trochocarpa cunninghamii* (DC.) Curtis | Epacridaceae |
| *T. gunnii* (Hook.f.) Benth. | Epacridaceae |
| *Zieria arborescens* Sims. | Rutaceae |